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Contents

Articles

489–497 **Barrientos, Claudio A., M. Teresa González, and Carlos A. Moreno**
Geographic differences in the feeding patterns of red rockfish (*Sebastes capensis*) along South American coasts

498–511 **Bergenius, Mikaela A. J., Gavin A. Begg, and Bruce D. Mapstone**
The use of otolith morphology to indicate the stock structure of common coral trout (*Plectropomus leopardus*) on the Great Barrier Reef, Australia

512–520 **Mant, Jason C., Michael J. Moran, Stephen J. Newman, S. Alex Hesp, Norman G. Hall, and Ian C. Potter**
Biological characteristics and mortality of western butterfish (*Pentapodus vitta*), an abundant bycatch species of prawn trawling and recreational fishing in a large subtropical embayment

521–532 **Butler, John, Melissa Neuman, Deanna Pinkard, Rikk Kvitek, and Guy Cochrane**
The use of multibeam sonar mapping techniques to refine population estimates of the endangered white abalone (*Haliotis sorenseni*)

533–541 **Scandol, James P., Tony J. Underwood, and Matt. K. Broadhurst**
Experiments in gear configuration to reduce bycatch in an estuarine squid-trawl fishery

542–549 **Love, Milton S., and Anne York**
The relationships between fish assemblages and the amount of bottom horizontal beam exposed at California oil platforms: fish habitat preferences at man-made platforms and (by inference) at natural reefs

550–558 **Corander, Jukka, Pekka Marttinen, and Samu Mäntyniemi**
A Bayesian method for identification of stock mixtures from molecular marker data

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559–570 **Shepherd, Gary R., Joshua Moser, David Deuel, and Pam Carlsen**
The migration patterns of bluefish (*Pomatomus saltatrix*) along the Atlantic coast determined from tag recoveries

571–578 **Seitz, Andrew C., Brenda L. Norcross, Derek Wilson, and Jennifer L. Nielsen**
Evaluating light-based geolocation for estimating demersal fish movements in high latitudes

579–584 **Burks, Carolyn M., William B. Driggers III, and Keith D. Mullin**
Abundance and distribution of whale sharks (*Rhincodon typus*) in the northern Gulf of Mexico

585–592 **Davis, Michelle L., and Jim Berkson**
Effects of a simulated fishing moratorium on the stock assessment of red porgy (*Pagrus pagrus*)

593–604 **Taylor, David L., Peter M. Rowe, and Kenneth W. Able**
Habitat use of the inner continental shelf off southern New Jersey by summer-spawned bluefish (*Pomatomus saltatrix*)

605–615 **Staudinger, Michelle D.**
Seasonal and size-based predation on two species of squid by four fish predators on the Northwest Atlantic continental shelf

Notes

616–622 **Rooper, Christopher N., Donald R. Gunderson, and David A. Armstrong**
Evidence for resource partitioning and competition in nursery estuaries by juvenile flatfish in Oregon and Washington

623–625 **LaPlante, Lori H.**
Length-specific brood size and winter parturition in pink seaperch (*Zalembius rosaceus*) (Perciformes: Embiotocidae)

626–630 **Riemer, Susan D., and Robert Mikus**
Aging fish otoliths recovered from Pacific Harbor seal (*Phoca vitulina*) fecal samples

631–637 **Thedinga, John F., Scott W. Johnson, and Donald G. Mortensen**
Habitat, age, and diet of a forage fish in southeastern Alaska: Pacific sandfish (*Trichodon trichodon*)

638–642 **Upadhyay, Satyendra K., Wang Jun, Su Yong-Quan, Ding Shao-Xiong, and Sonal Chaturvedi**
Genetic diversity of yellow grouper (*Epinephelus awoara*) determined by random amplified polymorphic DNA (RAPD) analysis

643–648 **Gregg, Jacob L., Delsa M. Anderl, and Daniel K. Kimura**
Improving the precision of otolith-based age estimates for Greenland halibut (*Reinhardtius hippoglossoides*) with preparation methods adapted for fragile sagittae

649 **Acknowledgment of reviewers**

650 **List of titles**

653 **List of authors**

655 **List of subjects**

Geographical differences in the feeding patterns of red rockfish (*Sebastes capensis*) along South American coasts

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Abstract—Feeding habits and feeding strategy of red rockfish (*Sebastes capensis*) were studied from fish captured along most of the range of this species in coastal waters of South America. Stomach contents of 613 individuals, collected during 2003, were analyzed. Fish were obtained from six locations along the Chilean (23°S to 46°S) and Argentinian (43°S) coasts. The main prey items were Mysidacea (75.06% IRI), Osteichthyes (6.29% IRI),and *Rhynchocinetes typus* (6.03% IRI). Predator sex and size did not significantly affect the diet, but significant differences were found between locations. Four geographical areas, discriminated by prey occurrence and frequencies, were determined: three on the Pacific coast and one on the Atlantic coast. These areas correspond roughly with biogeographic zones described for the Chilean and southern Argentinian coasts. The feeding strategy index (FSI) indicated a specialized feeding strategy for *S. capensis* for most of its range. However, the FSI does not include the behaviour of a predator, and the FSI must be interpreted carefully for fishes like *S. capensis* that are passive ambush feeders. The abundance and availability of different prey may explain both the geographic differences in dietary composition and the specialized feeding strategy of *S. capensis*.

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The feeding habits of a species, determined by its physiological, and behavioral adaptations, form a basic aspect of its biology; they provide a way to understand the trophic interactions between predators and their prey (Herrán[1]). Throughout the evolution of behavior and morphological adaptation there have been strong selective pressures toward those characteristics that allow a species to capture its prey and to escape from predators (Hixon and Beets, 1993; Reznick et al., 1997; Abrams, 2000).

Most trophic studies in fishes are carried out only on a local scale (e.g., Moreno and Zamorano, 1980; Ojeda and Fariña, 1996), and rarely consider the predator's entire distributional range. Thus, conclusions about the species' trophic patterns can reflect local conditions rather than a generalized feeding habit. In the Southern Hemisphere, red rockfish (*Sebastes capensis* (Gmelin, 1788)) is the only known species within this genus. It is distributed from the Pacific coast (the coast of Peru and Chile), to east of the Falkland Islands, to east of Tristan da Cunha, and as far as the southwestern coast of South Africa (Chen, 1971; Kong, 1985). *Sebastes capensis* is an ovoviviparous species that inhabits the waters over the continental shelf between 20 and 200 m in depth (Pequeño, 2000). Despite the economic importance of this species along the north and central coast of Chile, where it is exploited by local fisherman, there is little information about its biology and ecology. Currently, there is only one known study describing the diet of this species from the central Chilean coast (Ojeda and Fariña, 1996).

In our study, the feeding habits of *S. capensis* are described and its feeding strategy is analyzed along its geographic range in South America in order to understand whether the feeding pattern and the trophic behavior of this species are maintained at the regional scale. Moreover, the ability of the feeding strategy index of Amundsen et al. (1996) is evaluated for a predator like *S. capensis* that is a passive ambush feeder.

Materials and methods

Sampling

The area of study included most of the distributional range for *S. capensis* (Fig. 1) along the Chilean coast—Antofagasta (23°11′S; 70°29′W), Coquimbo (29°58′S;71°19′W), Val-

[1] Herrán, R. A. 1988. Stomach contents in fishes: bibliographic revision of objectives and methods. Technical report of the Instituto Oceanográfico Español, number 63, 74 p. Muelle de Poniente s/n; Apartado 291; 07015 Palma de Mallorca; Islas Baleares; Spain. [In Spanish.]

paraíso (32°54′S; 71°44′W), Talcahuano (36°44′S; 73°07′W), Valdivia (39°45′S; 73°08′W), and Aysén Fjord (45°34′S; 72°05′W—and in the Golfo Nuevo (42°45′S; 65°01′W) on the Argentinian coast.

Fish were captured between April and November of 2003. Details for each sampling period in each location are given in Table 1. The depths of capture varied from 15 to 50 m. Fish were captured 1) with hand lines from artisanal boats, 2) by submarine divers, or 3) they were acquired from local fishermen. Overall, a total of 613 specimens were analyzed, of which 375 were males and 238 were females.

Laboratory analysis

Immediately upon being captured, the fish were transferred from the sampling location to the laboratory, where they were frozen until analysis. The total length (TL) of each fish was measured to the nearest 1 cm of precision, total weight was recorded to the nearest 0.5 g precision), and sex was determined by macroscopic observation of the gonads.

The prey items found in the stomachs were sorted, counted, weighed, and identified to the lowest possible taxonomic level, according to Holthuis,[2] Garth,[3] Holmquist,[4] and Retamal (1981) for crustaceans, and according to Moreno and Castilla[5] for fishes.

Dietary analysis

Traditional methods of dietary analysis (counts, frequencies of occurrence, and weights of individual prey [Hyslop, 1980]) were used. These methods can either underestimate or overestimate the results. For this reason, a compound method of analysis was used. One of the most widely used compound indices in fish diet studies is the index of relative importance, IRI (Pinkas et al., 1971), which is expressed as a percentage, % IRI (Cortés, 1997). This index was calculated at the species and phylum level.

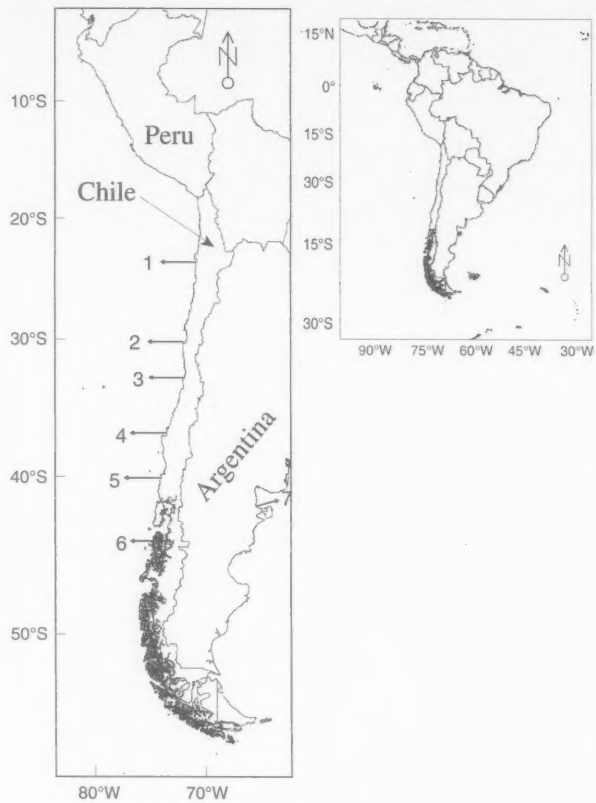

Figure 1

Sampling locations for red rockfish (*Sebastes capensis*) along the Chilean and Argentinian coasts. 1=Antofagasta, 2=Coquimbo, 3=Valparaíso, 4=Talcahuano, 5=Valdivia, 6=Aysen, and 7=Golfo Nuevo (Argentina).

Feeding strategy

The analysis of dietary composition proposed by Amundsen et al. (1996) was used.

This is based on a graphic representation; prey-specific abundance is plotted against the prey's frequency of occurrence on a two-dimensional space:

$$Pi = \frac{\sum Si}{\sum Sti} \times 100,$$

where Pi = the prey-specific abundance of prey i;
Si = the stomach contents (by weight) comprising prey i; and
S_{ti} = the total stomach contents (by weight) in only those predators with prey i in their stomachs.

This index gives information about prey importance (dominant versus rare) and the feeding strategy (gen-

[2] Holthuis, L. 1952. The Crustacea Decapoda Macrura of Chile. Reports of the Lund University Expedition 1948–49. Lunds Universitets Arsskrift 247(10):1–110. Lunds Universitets, Lund, Sweden.

[3] Garth, J. 1957. The Crustacea Decapoda Brachyura of Chile. Reports of the Lund University Expedition 1948–49. Lunds Universitets Arsskrift. number 7, 125 p. Lunds Universitets, Lund, Sweden.

[4] Holmquist, C. 1957. Mysidacea of Chile. Reports of the Lund University Expedition 1948–49. Lunds Universitets Arsskrift. number 6, 52 p. Lunds Universitets, Lund, Sweden.

[5] Moreno, C., and J. Castilla. 1978. Guide for the recognition and observation of fish from Chile. Expedition of Chile, 120 p. Universidad Austral de Chile, Casilla 567-Isla Teja, Valdivia, Chile. [In Spanish.]

Table 1

Sampling period and mean sizes (mean, in cm) of red rockfish *(Sebastes capensis)* examined by location and latitude. *n*=number of stomachs with prey; SD=size standard deviation, and *P*=probability associated with Kruskal-Wallis test. ns=no significant differences.

				Total length		
Location	Latitude	Sampling period	*n*	Mean	SD	*P*
Antofagasta	24°S	May–June 2003	29	24.8	1.74	ns
Coquimbo	30°S	May 2003	21	26.2	4.39	ns
Valparaíso	33°S	April–May 2003	50	22.2	3.02	ns
Talcahuano	36°S	April–May 2003	59	26.8	1.66	<0.05
Valdivia	40°S	April–May 2003	87	26.2	3.34	<0.05
Aysen fjord	45°S	July, November 2003	25	25.1	2.15	ns
Golfo Nuevo	43°S	June 2003	23	27.1	2.60	ns

eralist versus specialist) of the predator. The vertical axis of a hypothetical index represents the feeding strategy of the predator in terms of specialization or generalization. Prey points located at the upper left of the diagram would be indicative of specialization of individual predators, and those in the upper right would represent specialization of the predator population. Data seen in the upper right of the diagram (population specialization) necessarily restricted to a single point or to a few points, would reflect a predator population with a narrow niche diet. If all prey points were located along or below the diagonal from the upper left to the lower right, the predator population would have a broad niche width. Prey points located in either the upper left or the lower right corner would represent prey that make the same overall contributions to the population diet, but they would be indicative of totally different feeding strategies for the individual predators. Prey with high specific abundance and low occurrence (upper left) would be consumed by a few individuals displaying specialization, whereas prey with a low specific abundance and a high occurrence (lower right) would be eaten occasionally by most individuals. These differences in feeding strategy are related to the between- and within-phenotypic contributions to the niche width. In a population with a high between-phenotypic component, individuals specialize on different resource types. In a population with a high within-phenotype component, most of the individuals use many resource types simultaneously.

Statistical analysis

The Mann Whitney test was used to compare the sizes of fish between sexes, and the Kruskal-Wallis test was performed to compare the sizes of fish from different locations (Zar, 1999). The χ^2 contingency tables were used to evaluate the possible differences in the prey items clustered by phylum (Arthropoda, Chordata, and Mollusca) among locations. In addition, the *G*-statistic was used to evaluate differences in the occurrences of different prey types between sexes (Zar, 1999) and among the different size classes of fish defined arbitrary (class 1: fish between 18 and 25 cm, and class 2: fish between 26 and 38 cm) (Zar, 1999).

A correspondence analysis was used to evaluate the association between occurrences of prey items and the different locations, allowing the ordination of samples in a reduced space (two dimensions) (Digby and Kempton, 1987).

Results

Fish characteristics

A total of 613 specimens were analyzed and of those 296 stomachs contained some prey, 189 had empty stomachs, and 128 had everted stomachs (48.29%, 30.83% and 20.88%, respectively). Table 1 summarizes the characteristics of the fish analyzed by location. There was no significant difference in body size between males and females (U=9854.5, P=0.26). The size of fish differed significantly among locations: fish from Talcahuano and Valdivia did not differ significantly in size but were significantly larger than those from the others locations (Table 1).

Diet analysis

Across the geographical range, a total of 60 prey items were identified (Table 2): 40 crustaceans, 9 fishes, 3 cephalopods, 7 snails, and 1 polychetes. Crustaceans were the predominant prey in the diet of *S. capensis*. The low occurrence of other prey items allowed us to designate this species as carcinophagous (=feeding mainly on crustaceans).

Overall, the most important prey item was Mysidacea unident. (75.06% IRI), followed by Osteichthyes unident. (6.29% IRI), the rock shrimp *Rhynchocinetes typus* (6.03% IRI), deep red crab (*Petrolisthes desmarestii*) (4.67 % IRI), the rock crab *Cancer setosus* (2.32%

Table 2

Index of relative importance (IRI %) of each prey item recorded by location. Bold numbers show the most important prey items in each location. ANF=Antofagasta; COQ=Coquimbo; VAP=Valparaíso; THN= Talcahuano; VAD=Valdivia; AYS=Aysen channels; GNU=Golfo Nuevo. Unid.=unidentified.

Item prey	ANF	COQ	VAP	THN	VAD	AYS	GNU
Phylum Arthropoda							
Class Crustacea							
Rhynchocinetes typus	**40.76**	**92.15**	**27.38**	0.08			
Cancer setosus	1.17	0.17	**34.32**	5.09	0.19		
Cancer edwarsi				0.31			
Petrolisthes desmarestii	**48.68**	1.03	19.09	6.40			
Petrolisthes tuberculosus					0.29		
Pilumnoides perlatus	0.88	0.20	0.19	3.80	0.21		
Pagurus sp.		0.17					
Paguristes sp.				0.01			
Pagurus edwarsi			0.19		0.01		
Pagurus villosus						0.07	
Eurypanopeus crenatus					0.06		
Pseudocorystes sicarius						**94.63**	
Eurypodius latreillei				3.69	0.06		
Gaudichaudia gaudichaudi			0.46	0.01			
Taliepus sp.			0.21				
Pachycheles chubutensis							0.50
Pisoides edwardsi			0.25				
Pinnixa sp.						0.19	
Pterygosquilla armata		0.22			0.41		
Munida gregaria							**15.84**
Munida subrugosa							**32.07**
Halicarcinus planatus			0.65				**23.53**
Betaeus sp.	0..23						
Bateaus truncatus				**6.97**	0.04		
Synalpheus spinifrons	4.01		0.65				
Nauticaris magellanica			0.60	0.10	0.02		
Pleuroncodes monodon				0.04			
Austrapandalus grayi				0.04			
Exosphaeroma sp.							0.29
Mysidacea unid.				**71.94**	**92.13**		
Amphipoda unid.				0.05	0.005		
Euphausiacea unid.					0.002		
Alpheidae unid.				0.01			
Cirolanidae unid.							1.17
Porcellanidae unid.			0.23				
Cirripedia unid.				0.01			
Decapoda unid.		0.22					
Macruridae unid.			2.60	0.67	0.002	0.90	0.79
Braquiuridae unid.			0.65	0.61			

continued

Table 2 (continued)

Item prey	ANF	COQ	VAP	THN	VAD	AYS	GNU
Phylum Chordata							
Class Osteichthyes							
Engraulis ringens	0.52				0.37		
Chromis crusma		**3.54**		0.01			
Helcogramoides cumungamii					0.10		
Hipsoblennius sordidus					0.04		
Merluccius gayi				0.09			
Normanichthyes crokeri					0.06		
Odonthestes regia			0.25	0.01	0.36		
Osteichthyes unid.	1.25	2.12	8.49	0.03	**5.49**	**4.15**	**22.47**
Scorpaeniformes unid.					0.09		
Phylum Mollusca							
Class Cephalopoda							
Enteroctopus megalocyathus							0.74
Robsonella fontaniana			1.01				
Teuthoidea unid.					0.01		
Class Gastropoda							
Bittium peruvianum					0.002		
Turritella cingulata			2.60				
Nassarius dentifer	0.88						
Nassarius gayi	1.42						
Nassarius sp.		0.17					
Tricolia sp.				0.01	0.05		
Gastropoda unid.						0.03	1.17
Phylum Annelida							
Class Polychaeta							
Polychaetae unid.	0.21		0.19	0.03	0.002	0.03	1.19

IRI), and the megalop larvae of *Pseudocorystes sicarius* (1.78% IRI).

At the phylum level, the IRIs indicated that the most important prey group was Arthropoda (96.6%) followed by Chordata (2.93%), Mollusca (0.07%), and a low representation of Annelida (0.029%).

There were no differences between the sexes in the diet of *S. capensis*. Males and females both ate similar proportions of prey items (G=3.3; P>0.05). Neither sex was observed to show ontogenetic dietary changes: fish of the 19–25 cm size class, and fish between 26 and 38 cm TL showed no significant differences in prey items (G=2.27; P>0.05). On the other hand, there were significant differences in the diet of *S. capensis* among locations (χ^2=44.94, P<0.05). The correspondence analysis (Fig. 2) indicated that fish from Antofagasta, Coquimbo, and Valparaíso fed on similar prey items; whereas the fishes from Talcahuano and Valdivia fed mainly on other prey (Mysidacea spp.). Fish from the Aysén channels and the Argentinia coast showed qualitatively different diets. The diet of fish from the Aysén channels was characterized by the absence of those prey (e.g., *R. typus; P. desmarestii*) recorded in the fish from the northern locations. On the other hand, fish from the Argentina coast, fed on prey that are distributed only in higher latitudes (e.g., *Munida* spp.).

Table 2 summarizes the IRI % for each prey item in each location.

Antofagasta In this location, 29 specimens had stomach contents, from which 13 prey items were identified. The most important prey was the crab *P. desmarestii* (48.68% IRI), followed by the rock shrimp, *R. typus* (40.76% IRI), and low occurrences of shrimp *Synalpheus spinifrons* (4.01% IRI) and rock crab *C. setosus* (1.17% IRI).

Coquimbo Only 10 types of prey were identified from this location. The most predominant was *R. typus* (92.15%

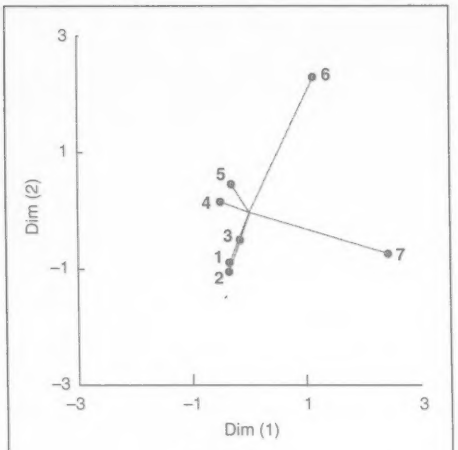

Figure 2

Compositional gradients of correspondence analysis of prey items (shown in Table 1) by location. 1=Antofagasta, 2=Coquimbo, 3 =Valparaíso, 4=Talcahuano, 5=Valdivia, 6=Aysen, and 7=Golfo Nuevo (Argentina). Dim (1)=dimension 1; Dim (2)=dimension 2.

IRI), followed by the fish *Chromis crusma* (3.54 % IRI) and unidentified Osteichthyes (2.12 % IRI). Polychaetes were not found in this area, and only one type of prey belonging to the phylum Mollusca was recorded.

Valparaíso Nineteen prey items were identified; of those, 14 were crustaceans. In this location, three prey items were predominant: the crab *C. setosus* (34.32% IRI), the shrimp, *R. typus* (27.38% IRI), and the crab, *P. desmarestii* (19.09% IRI). The fishes were relatively well represented (unidentified Osteichthyes 8.49% IRI). The Mollusca (2.60% IRI) were represented by the small octopus *Robsonella fontaniana,* and the snail *Turritella cingulata.*

Talcahuano A total of 24 prey items were identified from this location: 18 crustaceans, four fishes, one snail, and one polychaetae. The most important prey item was Mysidacea spp. (70.94% IRI), followed in importance by the crabs *P. desmarestii* (6.4% IRI) and *C. setosus* (5.09% IRI).

Valdivia Twenty four prey items were identified from this area. Mysidacea spp. was the most important in this location (92.13% IRI). However, six of the fish species we identified were represented in this area.

Aysén Fjord Despite the importance of unidentified prey items in this area, we observed an absence of most of the prey items found in the other locations. However, the trend of the predominance of crustaceans continued. The most important prey item was the megalop of *P. sicarius* (94% IRI) and unidentified Osteichthyes (4.15%). The larval stage of *P. sicarius* occurs seasonally; therefore, their importance in the diet of *S. capensis* from this geographical area can be associated with the sampling period (November).

Golfo Nuevo In this area, 12 prey items were identified. Lobster krill *Munida subrugosa* (32.07% IRI), the brachyuran crab *Halicarcinus planatus* (23.53% IRI), and *Munida gregaria* (15.84% IRI) were the most important prey items. The percentage of unidentified Osteichthyes (22.47% IRI) was higher than in other locations on the Chilean coast.

Feeding strategy

Figure 3 shows prey-specific abundance plotted against frequency of occurrence of prey items for *S. capensis* in the entire study area (Fig. 3A), and in each subarea (termed "location" in this article) (Fig. 3, B–H). This pattern of point distributions was similar for almost all locations. Most of the points (frequency of occurrence) were close to the left side of the x axis, and they tended to be positioned towards the upper left corner of the graph (specific abundance). There was a high between-phenotype contribution (BPC) to the niche width in Antofagasta (3B), Coquimbo (3C), Valparaíso (3D), Aysén fjord (3G), and Golfo Nuevo(3H) (i.e., individual predators specialized on different prey types and each food category was consumed by only a limited fraction of the predators). A more mixed feeding strategy, with varying degrees of specialization and generalization for different prey types was observed in Talcahuano (3E) and Valdivia (3F) (i.e., a high BPC and lower within-phenotype contribution (WPC) to the niche width). On the other hand, predominant prey items were observed only in Coquimbo, Valdivia, and Aysén fjord (*R. typus*, Mysidacea gen. sp., and the megalops of *P. sicarius,* respectively); rare or occasional prey items (crustaceans, fishes, mollusks, and polychaetes) were found in all locations.

Discussion

To determine the dietary variability of a predator, in order to describe its feeding pattern over its entire geographical range, is a difficult task because of the need for large sample sizes in a number of locations. Additionally, fish, such as *S. capensis,* whose percentages of empty or everted stomachs are high (50%), make an assessment of diet variability yet more difficult. We managed these difficulties by sampling fish during the same season, sampling over a similar depth range, and by using known information about the geographical distribution of prey items.

Geographical variation in the diet

The high percentage of crustaceans in the diet of *S. capensis* indicates that is primarily a carcinophagous fish,

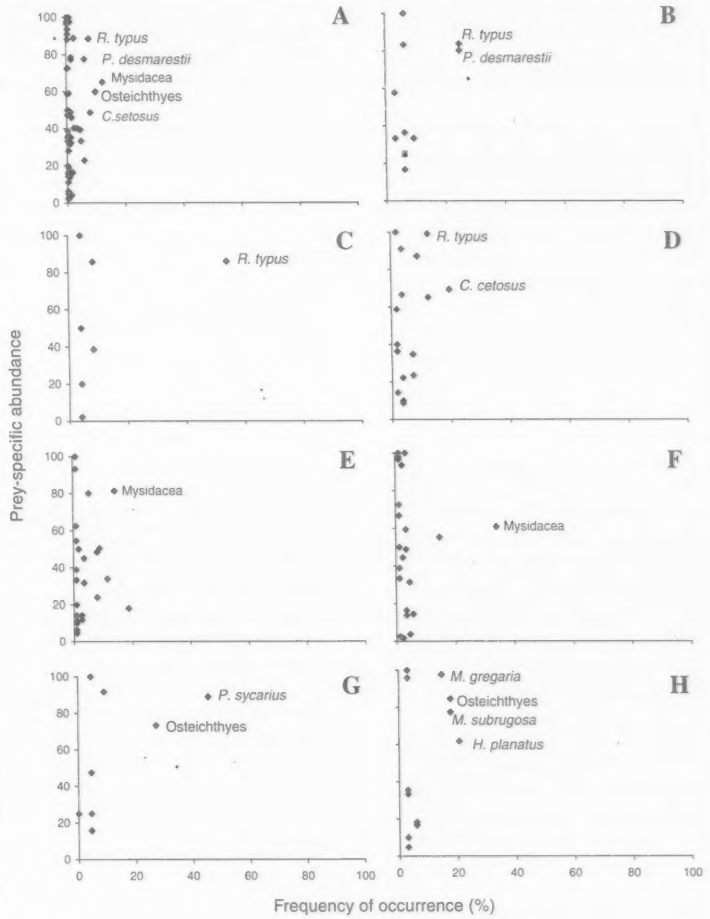

Figure 3

Prey-specific abundance (Pi) plotted against frequency of occurrence (%F) of prey items for red rockfish *(Sebastes capensis)* from the Chilean and Argentinean coasts. (**A**) entire geographic area, (**B**) Antofagasta, (**C**) Coquimbo, (**D**) Valparaíso, (**E**) Talcahuano, (**F**) Valdivia, (**G**) Aysen Fjord, and (**H**) Golfo Nuevo. *R. typus*= the rock shrimp *Rhynchocinetes typus*; *P. desmarestii*=deep red crab (*Petrolisthes desmarestii*); *C. setosus*=the rock crab *Cancer setosus; M. gregraria*=the lobster krill *Munida gregaria; M. subrugosa*=the lobster krill *Munida subrugosa; H. planatus*=the brachyuran crab *Halicarcinus planatus.*

and secondarily, a piscivorous species. Sixty prey items were recorded in the entire study area, including Mysidacea (75.06% IRI), the most important prey, followed by Osteichthyes (6.29% IIR), *Rhynchocinetes typus* (6.03% IRI), and *Petrolisthes desmarestii* (4.67% IRI).

The composition of prey species for *S. capensis* showed clear geographic variation. These changes were reflected by the relative importance of the different prey items in each of the study locations (Table 2) and were most evident in the fjords of Aysén and on the Argentinian coast, where all of the prey items found (except for *Halicarcinus planatus*) were unique to those locations. The crustacean *R. typus* was one of the most important prey items (50% IRI) between 23°S and 33°S. The rock shrimp *R. typus* is distributed from 10°S in Perú to 38°S on the Chilean coast (Retamal, 1981). Therefore, this prey species is not available on the southern Chilean coast (southward from 38°S). Between 37°S and 40°S,

Mysidacea was the most important prey item. In this geographic area, the mysids are also the most important prey item for other rocky bottom fishes (González and Oyarzún, 2003). Mysids are found in large and dense patches a few centimeters from the benthos (Silva and Stuardo, 1985).

The changes in prey types and their differences in IRI were also supported by a correspondence analysis (Fig. 2), which separated the sampling locations into four major areas according to recorded prey types as follows: 1) 23°S–33°S, 2) 37°S–40°S, 3) 45°S, and 4) Golfo Nuevo (43°S), Argentina. These geographic areas agree well with the proposed biogeographic units for this region by Briggs (1995) and by Camus (2001). According to Briggs (1995), two faunistic provinces are recognized in the southeastern Pacific: the Peruvian province, which extends from Perú (ca. 10°S) down to the northern Chilean coast (ca. 30°S), and the Magellanic province located on the southern Chilean coast (ca. 43°S). Between these provinces a transitional zone is found, in which species typical of the Peruvian province and the Magellanic province overlap (Brattström and Johanssen, 1983; Lancelloti and Vasquez, 2000). Additionally, Camus (2001) recognized five areas of distributional discontinuities along the Chilean coast: (1) 30°S; (2) 33°S; (3) 37°–38° S; (4) 41°–43°S, and (5) 52°–53°S. Thus prey, such as *R. typus,* are distributed along the Peruvian province and transitional zone, whereas prey like mysids are present mainly between latitudes 37°S and 40°S.

Alternatively, Balech (1954) and Pequeño (2000) considered all of South America's southern extremity as the same biogeographic province. The records of prey items (i.e., *Munida gregaria* and *M. subrugosa*) in Golfo Nuevo (Argentina coast) support the existence of a connection between the southeastern Pacific and the southwestern Atlantic. These prey species are also distributed along the Chilean coast from Chiloé (42°S) southward. However, these prey items were not found in Aysén fjord, which could be explained by the presence of two zones in the Aysen area with different physical and faunistic conditions: the fjord channels and a marine zone (Arntz et al., 1999). Fish were sampled in the Aysen channels, where species of *Munida* are absent (Retamal, 1981). Therefore, abundance and availability of prey may be a factor explaining the differences in the dietary composition of *S. capensis* between biogeographical regions.

The present study indicates the existence of geographic variations in the dietary composition of *S. capensis*, and these variations generally agree with the zoogeographic limits proposed in the literature. However, the interpretation of this result is limited because of the absence of an adequate background on the abundance and biogeography of each prey item.

Feeding strategy

According to Ojeda and Fariña (1996), *S. capensis* is a nocturnal predator that feeds selectively on the decapod crustaceans *R. typus* and *P. perlatus* in the rocky subtidal shores of the central Chilean coast. Ojeda and Fariña suggested that these species are consumed preferentially from a large array of potentially abundant invertebrate prey items. Crustaceans are more active at night than during the day, which could explain their large rate of consumption by rockfishes that are active a night. Decapod crustaceans have the highest caloric content (Duarte et al., 1980), therefore Ojeda and Fariña (1996) proposed that the specialized diet of *S. capensis* reflects an optimal foraging alimentary strategy based on the maximization of available energy. On the other hand, Moreno and Zamorano (1980) indicated that the feeding strategy of a species has a direct relationship with its morphological and behavioral adaptations that preclude being preyed upon, and these adaptations could restrict the potential prey items that they could capture. In this context, Moreno et al. (1979) and Moreno (1981) studied the bathymetric distribution of six species of fishes from the rocky subtidal shore of the Valdivian coast, including *S. capensis*. They established that the fishes segregate by habitats in order to take refuge from predators, mainly the sea lion *Otaria flavescens*; such segregation was not related to the bathymetric distribution of their most important prey items.

Sebastes capensis shows buccal traits characteristic of carnivorous species: it has a good protrusion capacity and its teeth are inclined in a dorsal-caudal orientation that prevents the escape of prey once they have been caught (Alvarado, 1985). *Sebastes capensis* is a poor swimmer; its anatomy conforms to that of sedentary species in that its head and mouth are big in comparison to the rest of the body, and it has big eyes that allow an extensive angle of vision facilitating the capture of their prey and the detection of their predators. Therefore, their capacity to catch prey depends mainly on characteristics of their prey. All prey species of *S. capensis* show similar behavioral traits (i.e., swimming organisms that move between rocky intertidal and subtidal zones) and *S. capensis* waits to capture them. The specialized feeding strategy of *S. capensis* may be a consequence of the availability of prey species moving in the vicinity of the refuges of this fish.

The feeding strategy index, as defined by Amundsen et al. (1996), has been used successfully for active predators like sharks (e.g., Lucifora et al., 2000; Vogler et al. 2003). However, this index does not integrate either predator behavior or the availability of prey in a given environment. Therefore, the criteria used to differentiate specialist from generalist predators must be clarified. According to the feeding strategy index of Amundsen et al. (1996), *S. capensis* is a specialized predator (preying mainly on crustaceans, although it consumes some prey species, and other rare prey species in almost all locations analyzed). In reality, *S. capensis* is an ambush predator that does not actively search for its prey. Because this fish waits in rocky refuges for mobile prey, the probability of it encountering prey depends, to a large extent, on prey abundances, prey distributions, and prey behaviors.

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The use of otolith morphology to indicate the stock structure of common coral trout (*Plectropomus leopardus*) on the Great Barrier Reef, Australia

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Abstract—We investigated the use of otolith morphology to indicate the stock structure of an exploited serranid coral reef fish, *Plectropomus leopardus*, on the Great Barrier Reef (GBR), Australia. Otoliths were measured by traditional one- and two-dimensional measures (otolith length, width, area, perimeter, circularity, and rectangularity), as well as by Fourier analysis to capture the finer details of otolith shape. Variables were compared among four regions of the GBR separated by hundreds of kilometers, as well as among three reefs within each region, hundreds of meters to tens of kilometers apart. The temporal stability in otolith structure was examined by comparing two cohorts of fully recruited four-year-old *P. leopardus* collected two years before and two years after a significant disturbance in the southern parts of the GBR caused by a large tropical cyclone in March 1997. Results indicated the presence of at least two stocks of *P. leopardus*, although the structure of each stock varied depending on the cohort considered. The results highlight the importance of incorporating data from several years in studies using otolith morphology to discriminate temporary and possibly misleading signals from those that indicate persistent spatial structure in stocks. We conclude that otolith morphology can be used as an initial step to direct further research on groups of *P. leopardus* that have lived at least a part of their life in different environments.

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Marine fish populations are generally distributed over large geographical ranges in a heterogeneous environment. Variable physical and biological processes may restrict the exchange of dispersive larvae and adults between areas within a population's species range, resulting in groups of individuals that are phenotypically or genetically distinguishable. Genetic and environmental processes may also have variable effects on the productive capacity (e.g., growth and reproduction) of individuals in different areas. Such variations may be directly measurable with variable life history characteristics, but also indirectly measurable with phenotypic characteristics, such as meristic and morphological characteristics.

Groups of individuals with different genetic or phenotypic characteristics can be defined as separate stocks. Although the precise definition of a stock has been widely debated (see reviews by MacLean and Evans, 1981; Begg, 1998; Booke, 1999), its ultimate meaning should depend on the management objective related to its use. If the management objective is to protect the genetic diversity of a species, for example, genetic information should be sought. If the purpose is to prevent over-fishing and localized depletion, information about life history characteristics is required. This information is needed because groups with different life history characteristics may respond differently to fishing pressure and therefore have different vulnerabilities to over-fishing (Cole, 1954; Adams, 1980; Jennings et al., 1998).

Variations in morphological characteristics of otoliths have proved useful for identifying stocks for a range of temperate marine fishes (e.g., Bird et al., 1986; Castonguay et al., 1991; Smith, 1992; Campana and Casselman, 1993; Friedland and Reddin, 1994; Begg et al., 2001; Smith et al., 2002), but have not been examined for tropical reef fishes. Differences in morphological characteristics between putative stocks indicate that the stocks have spent some periods of their lives in different environments (Begg et al., 1999; Cadrin, 2000) and therefore have the potential to develop different life history characteristics. Otolith morphological characteristics used as indicators of stock separation generally fall within one of three categories. The first category includes the traditional one-dimensional linear measurements of size-related attri-

butes, such as otolith length and width (e.g., Begg and Brown, 2000; Bolles and Begg, 2000) and distances between specific features on the otolith (e.g., Turan, 2000). Internal otolith measurements, such as nucleus length (e.g., Messeih, 1972; Neilson et al., 1985) and width of hyaline bands or increments (e.g., Begg et al., 2001) also fall within this category. The second category comprises two-dimensional size measurements, such as area, perimeter (e.g., Campana and Casselman, 1993; Begg and Brown, 2000; Bolles and Begg, 2000) and different shape indices, including circularity and rectangularity (e.g., Friedland and Reddin, 1994; Begg and Brown, 2000; Bolles and Begg 2000, Tuset et al., 2003). A third, more recent morphological technique examines the two-dimensional outline of otolith shape using Fourier analysis (e.g., Bird et al., 1986; Smith, 1992; Campana and Casselman, 1993; Begg and Brown, 2000; Smith et al., 2002). Fourier analysis produces a series of cosine and sine curves from the coordinates of a traced outline which, when added together, describe the outline of the traced form. The cosine and sine curves can be defined mathematically in a series of Fourier descriptors and used as variables to compare otolith shapes among individuals or potential stocks (Christopher and Waters, 1974; Younker and Ehrlich, 1977).

Plectropomus leopardus (common coral trout) (also known as leopard coralgrouper, FishBase[1]) is the most important commercially and recreationally harvested reef fish on the Great Barrier Reef (GBR), Australia (Mapstone et al.[2]; Williams[3]). *Plectropomus leopardus* comprises between 35% and 50% of the commercial reef line catch annually (Mapstone et al.[2]) and in 2004 a total allowable commercial catch (TACC) of 1300 t was implemented. Regional (hundreds of km) or inter-reef (hundreds to thousands of m) variations have been demonstrated in some life history characteristics of *P. leopardus* on the GBR (Begg et al., 2005), such as differences in density (Ayling et al.[4]), reproductive strategies (Adams, 2002), size and age (Russ et al., 1995; Lou et al., 2005), and mortality (Russ et al., 1995, 1998; Mapstone et al., 2004). Current management arrangements (such as TACC, fish size limits, gear restrictions, recreational bag limits, and spatial and temporal closures), however, do not incorporate the localized or regional spatial structure in the life history characteristics of *P. leopardus* or any other exploited species on the GBR.

The overall aim of this study therefore was to examine the use of otolith morphology for determining the stock structure of *P. leopardus* on the GBR. We investigated the broad spatial scale of *P. leopardus* by comparing aspects of otolith morphology among fish collected from four regions of the GBR, separated by hundreds of kilometers (north to south). Otolith structure was also assessed at finer spatial scales, among *P. leopardus* collected from neighboring reefs separated by hundreds of meters to tens of kilometers, within each of the four regions. In addition, because temporal variation in otolith shape could confound the spatial information if samples were taken from only one time, we also compared otolith morphological characteristics from two cohorts of *P. leopardus* with non-overlapping life histories either side of a significant environmental disturbance that affected the southern half of the GBR (the large and persistent Cyclone Justin in March 1997). Spatially variable effects of the Cyclone, such as a significant drop in temperature and salinity in large parts of the GBR (AIMS[5]), provided us with a unique opportunity to test the temporal stability of spatial patterns in otolith morphology.

Methods and data analysis

Background

Common coral trout (*Plectropomus leopardus*) were collected as part of the Cooperative Research Centre for the Great Barrier Reef World Heritage Area (CRC Reef) Effects of Line Fishing (ELF) experiment (Campbell et al., 2001; Mapstone et al., 2004). The ELF experiment, which began in 1995 and concluded in 2006, monitored line-caught fish populations from a group of six neighboring reefs in each of four regions extending over 7° of latitude along the GBR (Fig. 1; Mapstone et al.[6], 1996, 1997, 2004; Davies et al.[7]). At the start of the experi-

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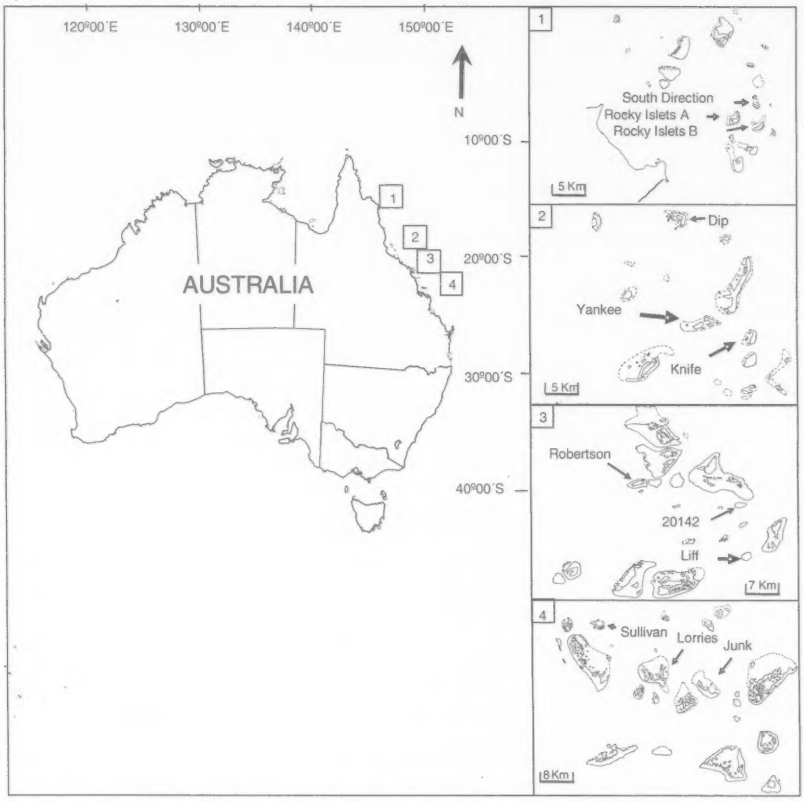

Figure 1

Great Barrier Reef, Australia. Study regions and reefs (1–4) from which common coral trout (*Plectropomus leopardus*) were collected are shown. 1 = Lizard Island; 2 = Townsville; 3 = Mackay; 4 = Storm Cay.

ment, four reefs in each region had been closed to fishing for 10–12 years under GBR Marine Park Zoning Plans (zoned Marine National Park B, MNP-B) and two reefs in each region had been open to fishing (zoned as General Use, GU). Two of the reefs closed to fishing remained closed during the experiment, other than to the annual research line fishing surveys. The other two closed reefs were each subjected to one year of fishing, in 1997 and 1999, after which they were closed again. The two reefs in each region that had historically been open to fishing were subjected to increased fishing pressure for one year (i.e., were temporarily opened). These reefs were then closed for five years before reverting to their original zoning status (GU).

All reefs were sampled each year in the austral spring (October–December) to coincide with the peak spawning period of the main target species, *P. leopardus*. Each reef was divided into six approximately equal-size, contiguous blocks, and sampled on a single day on each sampling occasion. Standardized commercial reef line fishing effort was distributed uniformly across two depth strata within each block. All fish caught were measured, tagged for later identification, and kept for weighing and for extraction of gonads and otoliths. For further sampling details of the ELF experiment see Davies et al.[7] and Mapstone et al. (2004). Samples of *P. leopardus* were aged by CRC Reef staff using standardized methods developed by Ferreira and Russ (1994).

Sample collection

Otolith morphological variables were analyzed from four-year-old *P. leopardus* collected in 1995 and 1999 from three reefs within each of the four regions (Fig. 1; Table 1). Four years is the youngest age at which *P. leopardus* in all regions are fully recruited to the fishing gear used in the ELF Experiment. Although the zoning status of a reef and the level of fishing pressure on it were unlikely to have affected otolith structure, one reef from each treatment regime in the ELF experiment was included from each region to avoid potential biases in spatial variation related to particular fishing histories. Thus, within each region, samples were analyzed from one MNP-B reef that was closed to fishing, one MNP-

Figure 2

Example of a common coral trout (*Plectropomus leopardus*) otolith reconstructed by using (**A**) all of the 128 Fourier descriptors that were collected, and (**B**) the first and last 14 descriptors. Otolith orientation and measures of length and width are indicated.

Table 1

Study regions, reefs, and years for which the common coral trout (*Plectropomus leopardus*) was sampled over the Great Barrier Reef and examined for otolith morphology.

Region	Reef (GBRMPA number)	1995, 1999 replicates	Total length range (mm)
Lizard Island	Rocky Islet Reef A (14132a)	20, 6	304–495
	Rocky Islet Reef B (14132b)	20, 6	306–481
	South Direction Reef (14147)	20,12	350–468
Townsville	Knife Reef (18081)	8, 4	370–451
	Dip Reef (18039)	7,12	318–462
	Yankee Reef (18074)	20, 8	322–464
Mackay	unnamed reef (20142)	20, 18	322–456
	Liff Reef (20296)	20, 16	303–427
	Robertsqn Reefs (no2) (20136)	20, 11	342–514
Storm Cay	Junk reef (21131)	20, 15	345–422
	Lorries reef (21130)	20, 11	328–475
	Sullivan reef (21124)	18, 19	280–424
Total		213, 138	303–514

B reef that was open for one year of fishing and then closed, and one GU reef that was subjected to increased fishing for a year prior to closure for five years.

Because otoliths from only four-year-old fish were analyzed in 1995 and 1999, the two cohorts included individuals with nonoverlapping life histories. Consequently, individuals collected in 1995 were not exposed to the influence of the unusually large and persistent Cyclone Justin that influenced the southern half of the GBR throughout March in 1997, unlike those four-year-old fish collected in 1999. Standardizing sampling by age also minimized the potential for confounding spatial variation in otolith shape with ontogenetic changes.

Sagittal otoliths from up to 20 four-year-old *P. leopardus* were sampled from each reef each year (Table 1). Otoliths from fewer than 20 fish were analyzed only if less than this number were collected from a reef. This sampling design enabled the examination of broad (region) and fine (reef within region) spatial and temporal (1995 and 1999 cohorts) patterns in the otolith morphology of *P. leopardus* across much of the GBR, spanning an unusual environmental event (Cyclone Justin, 1997) that had the potential to significantly influence the results.

Morphological analysis

A microscope image (10× magnification) was projected onto a computer screen by using a video camera (Panasonic GP-KR222E, Panasonic, Matsushita Communication Industrial Co., Osaka, Japan. Whole otolith area, length, perimeter, and width (Fig. 2) and two shape indices (circularity and rectangularity) were recorded from each otolith by using the OPTIMAS image analysis system (OPTIMAS, vers. 6.51, Silver Spring, MD). Rectangularity was calculated as the area of the otolith divided by the area of its minimum enclosing rectangle, and circularity as the perimeter of the otolith squared divided by its area. The perimeter of the otolith was traced in a counter clockwise direction and digitized into 128 *x-y* equidistant coordinates by using the distal edge of the otolith rostrum as a common starting point

for the coordinates. A fast Fourier transform (FFT) was calculated as a Cartesian FFT. The Cartesian FFT uses the 128 *x-y* coordinates as complex numbers ($a + ib$), where a is the real component and ib the imaginary component, representing the amplitudes of the cosine and sine waves, respectively. The resultant 128 set of complex numbers or descriptors were subsequently normalized for differences in otolith position by setting the 0^{th} descriptor to 0, and for size and rotation of the otolith by dividing all the descriptors with the first descriptor. The normalized descriptors ($a' + ib'$) were used to calculate the absolute value (harmonic) of each descriptor according to the following equation (Christopher and Waters, 1974):

$$Harmonic = \sqrt{a_n'^2 + (ib')_n^2}.$$

The harmonics were then used in combination with the other morphological variables and shape indices to compare otoliths between cohorts and among regions and reefs within regions.

The higher the number of equidistant points and subsequent complex numbers included in the model, the closer is the fit to the original shape. The main features of the otolith shape, however, are generally captured by the first 10–20 harmonics (e.g., Campana and Casselman, 1993; Friedland and Reddin, 1994). The minimum number of Fourier descriptors required to explain at least 90% of the recorded shape of the otoliths in our study was calculated similarly to the range-finding procedure of Smith et al. (2002). A total of 128 descriptors were collected from two randomly selected otoliths from each reef and cohort (24 in total) and normalized for position, size and rotation as described above. The shape of each otolith was reconstructed (by computing the inverse FFT) by using all the descriptors and then reconstructed by using only the first and last descriptors. The Euclidian distance between the inverse FFT using all the descriptors and the inverse FFT using only the first and last descriptors was defined as the maximum percent error of reconstruction, i.e. 100% reconstruction error (Smith et al., 2002). Because the Cartesian descriptors are asymmetrical around the middle frequency, both ends of the array are required in the reconstruction. Otolith shape was reconstructed, therefore, by using the first two and last two descriptors, the first three and last three descriptors, and so on until the first and last 22 descriptors were used. This range-finding test allowed us to estimate the decrease in mean percent reconstruction error by using more and more descriptors and it was estimated that 14 of the first and last descriptors were required for the reconstruction error to be less than 10%. See Figure 2 for a comparison of the otolith shape reconstructed from the first and last 14 descriptors and all 128 descriptors. These descriptors, therefore, were used in the statistical analyses to compare the spatial and temporal patterns in otolith shape of *P. leopardus*.

Statistical methods

The assumption of normality and homogeneity of variance for each morphological variable was examined by using Shapiro-Wilk's and Levene's tests, respectively, and homogeneity of the group covariance matrix by Box's M test. Variables of circularity, breadth and area were $\log_{10}$-transformed and Fourier harmonics 2, 4, 9, 11–14, 120–121, 114–118, and 123–127 square-root–transformed to conform to the assumption of normality and homogeneity of variances.

A relationship between otolith shape and otolith growth rate (assumed to be correlated to fish length) may confound spatial or temporal differences in otolith shape (Campana and Casselman, 1993). We minimized the potential for such effects by 1) including only fish with a fork length (FL) between 280 and 514 mm (overall FL for four-year-olds sampled during the ELF experiment in 1995 and 1999 ranged from 250 to 551 mm), and 2) standardizing morphological variables by fish FL where a significant relationship existed between the variable and FL before further analyses. The effect of FL on each morphological variable was examined by analysis of covariance (ANCOVA; Winer et al., 1991). Our primary interests in these analyses were 1) to test whether morphological variables differed with FL for any group of samples; and 2) if so, to test whether the slopes of regressions of morphological variable on FL were homogeneous among groups. If a significant regression was detected and homogeneous among groups, the effect of FL was removed from each measurement by using the relationship

$$O_{ij,adj} = O_{ij} + b.(FL_{ij} - MFL._j).$$

where $O_{ij,\,adj}$ = otolith morphological measurement of fish i adjusted to mean fork length of group j;
O_{ij} = original otolith morphological measurement for fish i from group j;
$b.$ = slope of the relationship O_{ij}:FL_{ij} common to **all** groups;
FL_{ij} = fork length of fish i in group j; and
$MFL._j$ = average fork length within group j.

If significant slopes of the relationship differed among groups, the correction for FL was made separately for each group by using the equation above, but by replacing the common slope ($b.$) with the group-specific slope (b_j). These corrections had the effect of scaling all morphological variables from all otoliths to their predicted group mean FL.

Multivariate analysis of variance (MANOVA; Tabachnick and Fidell, 1983) was used to investigate the effects of sex (females, males, and individuals in the process of changing sex; i.e., transitional fish) on otolith shape (MANOVA). A total of 302 of the 351 individuals had been examined for sex, of which 166 were females, 123 males and 13 transitional fish. Separate MANOVAs were computed for the one- and two-dimensional shape

variables and the Fourier harmonics by using a three-way crossed model (outlined below) with fixed factors: cohort, region, and sex. Data were pooled across reefs within regions owing to insufficient sample numbers to test for reef-specific effects.

A MANOVA was used to test for spatial and temporal differences in otolith shape. A principal component (PC; Tabachnick and Fidell, 1983) analysis was done first on the combined data set of both the shape variables and Fourier harmonics to reduce the number of variables to be incorporated in the MANOVA. The number of PCs to extract and subsequently include in the MANOVA was determined by examining the size of the eigenvalues (representing the variance explained by each PC), as well as their relative contribution to the percent variance explained compared to the other eigenvalues (i.e., scree test; Tabachnick and Fidell, 1983). The latter determines the number of PCs beyond which the addition of more PCs would contribute little to the variance explained by the solution (Tabachnick and Fidell, 1983). Wilk's lambda criterion was used to test for group differences in the MANOVAs. Sums of squares and degrees of freedom of interactions were pooled when the *F*-ratios of interaction effects were ≤1. Pooling increases the degrees of freedom for the denominator and consequently the power of the test of remaining (unpooled) effects in the analyses.

A posteriori univariate analysis of variance (ANOVA) was used to explore patterns for each of the PCs separately when significant effects were indicated in the MANOVA. The univariate linear model for the analysis of each PC was

$$x_{ijkl} = \mu_{....} + C_{i...} + R_{.j..} + r(R)_{.k(j)} + CR_{ij..} + Cr(R)_{ik(j).} + e_{l(ikj)},$$

where x_{ijkl} = the PC score for otolith l from cohort i, region j and reef k;

$\mu_{....}$ = the estimate of the population mean PC score over all cohorts, regions, reefs, and otoliths;

$C_{i...}$ = the fixed effect of cohort i averaged over regions and reefs;

$R_{.j..}$ = the fixed effect of region j averaged over cohorts and reefs;

$r(R)_{.k(j)}$ = the random variation attributable to reef k within region j averaged over cohorts; and

$e_{l(ikj)}$ = unexplained random variation associated with otolith l within cohort i, region j and reef k.

Tukey's honestly significant difference (HSD) test was used to determine which means differed following significant effects detected in the ANOVAs. The communalities (representing the proportion of the total variance of a variable accounted for by the PC) and variable loadings of the PCs that were significant in the ANOVAs were subsequently examined. A loading below 0.45 indicated that the variable explained less than 20% of the PC and therefore was not interpreted further.

Finally, two forward stepwise canonical discriminant analyses (CDAs; Tabachnick and Fidell, 1983) were computed by using the shape variables and Fourier harmonics to examine the otolith shape of *P. leopardus* in multivariate space and to investigate whether otolith shape could be used to classify samples to spatial scale and cohort of origin. The factor used as a separating variable in the CDA depended on the significant effects determined in the MANOVA (i.e., cohort, region, or reef [region], or any interactions between these factors). The CDA was used in this way as a confirmatory technique. Wilk's lambda criterion was used to test for significant differences between the discriminant functions. Jackknife classification was used to minimize potential bias in the reclassification of individuals.

Results

Slopes of the relationship between FL and several otolith morphological variables for *P. leopardus* differed among a range of spatial scales and between cohorts (Table 2). The within-group slope, therefore, was calculated for each group according to the level at which the slopes of the relationship differed and was used to correct for the influence of FL (Table 2). For some variables, the common between-group slope was used to correct for the influence of FL because there was a significant overall relationship between the variable and FL, which was homogeneous among groups (ANCOVA homogeneity of slopes test, $P>0.05$; Table 2). No morphological variable was significantly correlated with FL after standardization. Furthermore, shape variables and Fourier harmonics were not significantly different between otoliths of females, males or transitional fish (MANOVA, $P>0.05$). The morphological data, therefore, were pooled across sex for the remainder of the analyses.

Principal component analysis (PCA)

Four PCs were extracted from the analysis of the combined data set of shape variables and Fourier harmonics and included in the MANOVA (Table 3). The communalities ranged between 0.11 and 0.88, and some morphological variables were better defined by the PC solution than others (Table 3). About 44% of the total variance in the morphological data was explained by the four extracted PCs (17.9%, 10.2%, 9.9% and 5.9% by PC I, II, III, IV, respectively). A combination of higher order harmonics describing the finer details of the otolith outline, and lower order harmonics, perimeter, length, and circularity representing the broad shape of otoliths explained most of the variation in PC I and III (Table 3). Variation in the broader details of otolith shape also accounted for most of the variation in PC II and PC IV; otolith area, breadth, perimeter, length, and harmonic eight explained most of the variation in PC II and breadth and harmonic 127 explained most of the variation in PC IV (Table 3).

Table 2

Results of the homogeneity of slopes test for the influence of fish fork length (FL) on otolith morphological variables of four-year-old *Plectropomus leopardus*. The level of correction represents the level at which the slopes were heterogenous. For example, the level of correction "reef(region)" means that the slopes of the relationship between FL and a morphological variable differed among reefs nested within regions and that the slope for each reef was used to correct for the influence of FL. Level of correction "FL" means that there was a significant overall relationship between FL and a morphological variable, but that the slopes of this relationship were homogenous among reefs(region), regions and cohorts. Only variables with a statistically significant relationship with FL are shown.

Variable	df	F	P	Level of correction
Log_{10} breadth	8, 306	1.99	0.0467	reef(region)
Log_{10} circularity	8, 306	1.99	0.0479	reef(region)
Length	3, 315	4.05	0.0075	region
Log_{10} area	8, 306	2.01	0.0452	reef(region)
Perimeter	8, 306	2.34	0.0187	reef(region)
Rectangularity	1, 341	14.43	0.0002	FL
Sqrt harmonic 2	1, 349	11.15	0.0009	FL
Harmonic 3	1, 349	10.32	0.0014	FL
Sqrt harmonic 4	1, 349	6.90	0.0090	FL
Harmonic 5	3, 314	3.44	0.0171	cohort × region
Harmonic 6	7, 314	2.12	0.0410	reef(region)
Harmonic 7	1, 349	13.56	0.0003	FL
Sqrt harmonic 9	7, 307	2.30	0.0270	cohort × reef(region)
Sqrt harmonic 13	1, 349	8.05	0.0048	FL
Sqrt harmonic 14	7, 317	3.31	0.0021	reef(region)
Sqrt harmonic 114	1, 327	8.69	0.0034	vohort
Sqrt harmonic 115	7, 307	2.48	0.0170	cohort × reef(region)
Sqrt harmonic 116	7, 317	3.95	0.0004	reef(region)
Sqrt harmonic 117	7, 317	2.89	0.0061	reef(region)
Sqrt harmonic 118	3, 314	2.90	0.0354	cohort × region
Harmonic 119	1, 349	6.79	0.0096	FL
Sqrt harmonic 120	3, 325	2.91	0.0346	region
Sqrt harmonic 121	7, 307	2.10	0.0435	cohort × reef(region)
Harmonic 124	3, 314	4.01	0.0080	cohort × region
Harmonic 125	1, 349	10.79	0.0011	FL
Harmonic 126	1, 349	31.76	<0.0001	FL
Harmonic 127	1, 327	4.37	0.0373	cohort

The MANOVA of the four PCs identified significant differences in the PC scores of otolith shape among regions, but were not consistent between cohorts (1995 and 1999; cohort×region interaction, Table 4). Univariate ANOVAs indicated that these differences were due to variation in PC II among regions and in PC IV among reefs within regions—both spatial patterns varying depending on the cohort in consideration (Table 5). Differences in PC II were due to differences between Lizard Island and Mackay regions in 1995 and between cohorts in Mackay (Fig. 3A; HSD, $P<0.05$). The apparent inconsistency between the significant reef within region effect in the ANOVA (PC IV) and no such reef effect detected in the MANOVA is most likely explained by the difference between two reefs in the Lizard Island region, for which there was a significantly lower mean PC IV score for Reef 14132a than for Reef 14147 in 1995, whereas the reverse was observed in 1999 (Fig. 3B; HSD, $P<0.05$). There was also a significant difference among cohorts on Reef 14132a (Lizard Island) and Reef 20296 (Mackay Region; Fig. 3B; HSD, $P<0.05$).

Although only explaining 18% (PC II and PC IV combined) of the variation in our morphological data, the PC analysis indicated that the presence of at least two stocks of *P. leopardus* on the GBR in 1995, one in the northern part of the GBR (Lizard Island) and one in the southern part (Mackay), whereas one homogeneous stock was indicated in 1999.

Table 3

Variable communalities and loadings on the four significant principal components (PCs) explaining 44% of the total variance in the otolith morphological data of four-year-old *Plectropomus leopardus* collected from three reefs in each of four regions in 1995 and 1999 on the Great Barrier Reef.

		Loadings			
Variable	Communalities	PC I	PC II	PC III	PC IV
Perimeter	0.88	0.39	0.69	0.51	0.01
Length	0.85	0.07	0.57	0.71	0.14
Log_{10} area	0.81	−0.05	0.80	0.32	−0.27
Log_{10} breadth	0.80	−0.03	0.70	−0.10	−0.55
Harmonic 127	0.78	0.18	−0.16	0.65	0.55
Log_{10} circularity	0.76	0.67	0.13	0.42	0.33
Sqrt harmonic 4	0.70	0.80	0.04	−0.21	−0.09
Harmonic 6	0.64	0.72	0.18	−0.27	−0.11
Harmonic 5	0.58	0.63	−0.29	0.27	−0.15
Harmonic 8	0.51	0.17	0.57	−0.38	0.09
Harmonic 10	0.49	−0.32	0.44	−0.29	0.34
Sqrt harmonic 2	0.49	0.70	0.00	−0.04	0.03
Harmonic 3	0.49	−0.40	−0.05	0.57	0.01
Harmonic 122	0.45	0.43	0.40	−0.25	0.21
Sqrt harmonic 13	0.44	0.58	−0.08	−0.07	−0.30
Sqrt harmonic 117	0.41	0.42	−0.21	0.11	−0.42
Harmonic 7	0.41	0.54	−0.23	0.06	0.25
Sqrt harmonic 120	0.40	0.37	0.26	−0.32	0.30
Sqrt harmonic 11	0.37	0.54	−0.12	0.03	−0.25
Harmonic 119	0.37	0.45	−0.30	0.22	−0.14
Harmonic 125	0.35	−0.22	0.02	0.55	0.03
Sqrt harmonic 115	0.35	0.33	−0.12	0.22	−0.42
Sqrt harmonic 121	0.31	0.39	−0.37	0.16	−0.01
Harmonic 124	0.30	0.48	0.11	0.03	0.24
Sqrt harmonic 116	0.26	0.30	0.14	−0.35	0.18
Sqrt harmonic 118	0.26	0.49	0.02	−0.11	0.06
Sqrt harmonic 114	0.18	0.19	0.00	−0.37	0.10
Sqrt harmonic 12	0.18	0.22	−0.11	0.33	−0.05
Harmonic 126	0.16	0.32	0.18	0.04	0.13
Sqrt harmonic 9	0.14	0.09	−0.20	−0.05	0.30
Sqrt harmonic 123	0.14	0.27	−0.03	−0.17	0.18
Rectangularity	0.13	−0.25	−0.17	−0.18	0.08
Sqrt harmonic 14	0.11	0.30	−0.09	−0.02	0.10

Discriminant analyses

Two stepwise canonical discriminant analyses (CDAs) were computed for the morphological variables (Fourier harmonics and shape variables combined) in response to the significant cohort × region effect in the MANOVA of the PC scores. First, separate CDAs were done for each region using cohort as the separating variable and second, separate CDAs were done for each cohort by using region as the separating variable. The region-specific CDA, where cohort was used as a separating variable, showed a significant first discriminant function (DF) for all four regions, accounting for 100% of the variance in the data (Table 6). Some separation was observed in the distribution of the DF I scores between the two cohorts within each region, although the temporal pattern was not consistent across regions (Fig. 4). Likewise, the cohort specific CDA using region as a separating variable showed some separation between the four regions in the first two significant DFs of cohort 1995 (explaining 59.9% and 30.7% of the variance, respectively) and one significant function of cohort 1999 (explaining 100% of the variance, Table 6). The means of the DF I scores in the Lizard Island and

Townsville regions were distinctly greater than those of the Mackay and Storm Cay regions in 1995 (HSD, $P<0.05$; Fig. 5A) and in Townsville were greater than the Mackay and Storm Cay regions in 1999 (HSD, $P<0.05$; Fig. 5B).

Different combinations of harmonics 9, 114, 118 describing the finer details of the otolith shape, and harmonic 124 and shape variables area and circularity representing the broad details of otolith shape, were selected into the DFs to maximize the separation of cohorts within regions (Table 7). The primary predictor variables selected for separating regions in each of the cohorts were similar to those selected in the region-specific CDA, although the variables were not the same in each cohort (Table 7). Between 66.7% and 76.3% of *P. leopardus* within a region could be correctly classified to their cohort of origin (Table 8). Fewer cohort specific individuals could be classified to a region however;

Table 4

Results of MANOVA comparing principle component (PC) I–IV scores of otolith shape from two cohorts of four-year-old *Plectropomus leopardus* collected from three reefs in each of four regions in 1995 and 1999 on the Great Barrier Reef. *P*-values in bold indicate significant differences ($P<0.05$).

Factor	Wilks' lambda	*F*	df	*P*
Cohort	0.3800	2.04	4, 5	0.2269
Region	0.0513	2.34	12, 14	0.0687
Cohort×region	**0.0315**	**3.04**	**12, 14**	**0.0269**
Reef(region)	0.8880	1.19	32, 1167	0.2126
Cohort×reef(region)	0.8900	1.18	32, 1167	0.2318

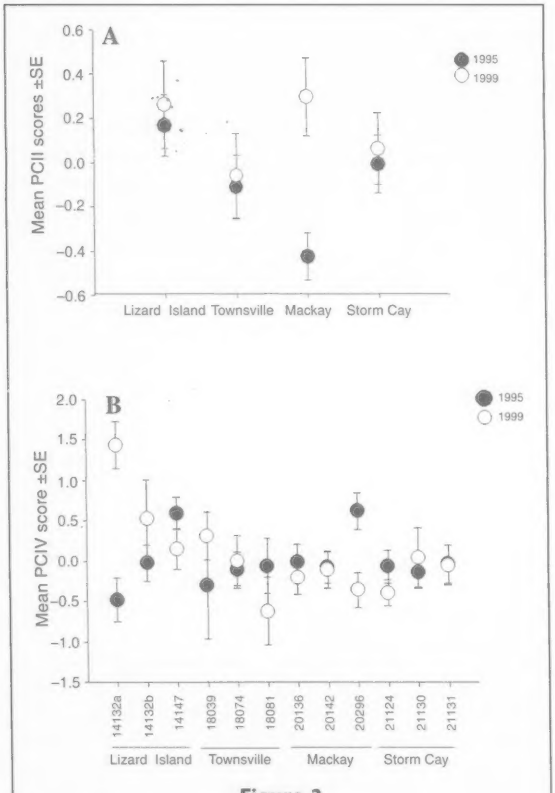

Figure 3

Mean (**A**) principal component (PC) II scores per region and cohort, and (**B**) PC IV scores per reef within region and cohort of four-year-old common coral trout (*Plectropomus leopardus*), collected from three reefs in each of four regions in 1995 and 1999 on the Great Barrier Reef.

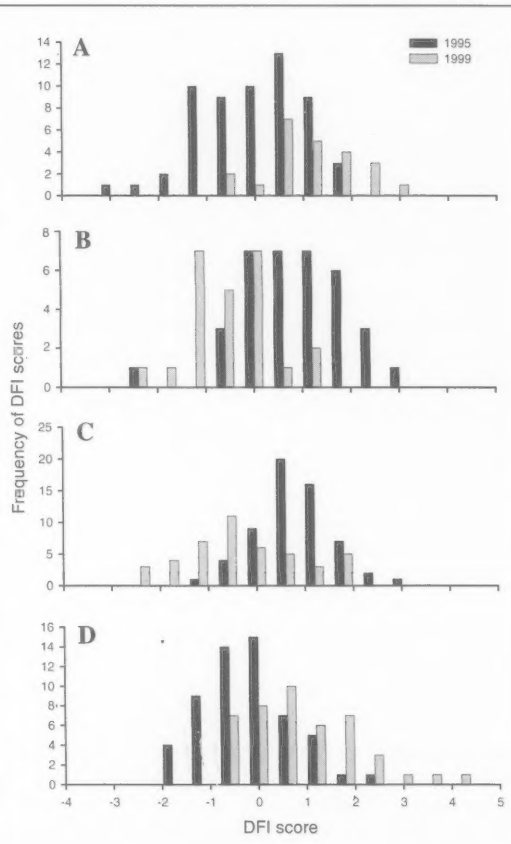

Figure 4

Frequencies of discriminant function (DF) I scores from otolith morphological variables (Fourier harmonics and shape variables combined) per cohort (sampled in 1995 and 1999) for regions (**A**) Lizard Island, (**B**) Townsville, (**C**) Mackay, and (**D**) Storm Cay for four-year-old common coral trout (*Plectropomus leopardus*), from the Great Barrier Reef. (The data were pooled across reefs within regions.)

34.3% and 39.7% were correctly classified for cohorts sampled in 1995 and 1999, respectively (Table 9).

Discussion

Spatial and temporal variation in otolith structure

This study detected differences in the otolith shape of *P. leopardus* at different spatial and temporal scales across the Great Barrier Reef (GBR), Australia. Although the spatial patterns in otolith shape of *P. leopardus* were not always consistent among different types of shape variables, two main inferences can be made from our results. Firstly, our results indicate that otolith morphology can be useful for identifying groups of individuals of this species that are likely to have spent a significant part of their lives in different environments and therefore may indicate potential stock separation. Overall otolith shape suggested the presence of at least one southern and one northern stock along the GBR. The Storm Cay and Mackay regions consistently belonged to the southern stock and the Lizard Island region to the northern stock, and it was inconclusive as to which stock individuals in the Townsville region belonged. It is possible that the main morphological features of otoliths are established in the larval stage and that large amounts of larval dispersal and mixing between areas results in overlap of signatures between stocks. Finer details of otolith shape, however, are most likely influenced by environmental processes during the post larval phase and may therefore provide insights to the separation of stocks during postlarval life.

Although otolith shape also suggested variation at a smaller, among reef, spatial scale (hundreds to thousands of m) the significant differences in the multivariate morphological measurement (PC IV) occurred only between two reefs in the Lizard Island region, and therefore it seems unlikely that such small-scale separation is a common phenomenon on the GBR. Nevertheless, the presence of some difference among reefs emphasizes the importance of careful and sufficient sampling in order to capture the range of values manifest in small-scale, presumably random, variation within regions and to avoid erroneously ascribing to regional structure what are really a reflection of local-scale variation. Given the hydrodynamic mixing over scales of kilometers, we consider it unlikely that reef-scale variations in morphological variables represent persistent environmentally induced patterns in stock structure.

Table 5

Results of ANOVAs comparing otolith principle component (PC) scores of otolith structure from two cohorts of four-year-old *Plectropomus leopardus* collected from three reefs in each of four regions in 1995 and 1999 on the Great Barrier Reef. Only final analyses resulting from pooled terms with $F \leq 1$ are shown. *P*-values in bold indicate significant differences ($P<0.05$). Only PCs with significant differences are shown. MS=mean square.

Variable	Factor	df	MS	*F*	*P*
PC II	Cohort	1	1.5165	1.60	0.2067
	Region	3	0.8057	0.47	0.7126
	Reef(region)	8	1.7209	1.82	0.0732
	Cohort×region	**3**	**3.0900**	**3.26**	**0.0217**
PC IV					
	Cohort	1	0.3246	0.11	0.7473
	Region	**3**	**3.2901**	**8.11**	**0.0083**
	Cohort×region	3	3.5574	1.21	0.3675
	Reef(region)	8	0.4059	0.43	0.9011
	Cohort×reef(region)	**8**	**2.9452**	**3.14**	**0.0020**

Table 6

Significance test of cohort-specific and region-specific canonical discriminant analysis (CDA) of shape variables and Fourier harmonics combined from otoliths of four-year-old *Plectropomus leopardus* collected from three reefs in each of four regions in two cohorts, 1995 and 1999 on the Great Barrier Reef. Only significant discriminant functions (DF) are shown. DF=discriminant function; df=degrees of freedom.

Scale	Factor	DF	Wilks' lambda	χ^2	df	*P*
Spatial scale						
Lizard Island	Cohort	I	0.7818	19.21	2	<0.0001
Townsville	Cohort	I	0.6863	20.89	3	0.0001
Mackay	Cohort	I	0.7685	26.34	4	<0.0001
Storm Cay	Cohort	I	0.7683	25.43	3	<0.0001
Temporal scale						
1995	Region	I to III	0.7573	56.72	12	<0.0001
1995	Region	II to III	0.8918	23.36	6	0.0006
1999	Region	I	0.91	11.95	3	0.0075

The second inference from our results is that regional patterns in otolith shape are not always consistent among cohorts and may be subject to temporally dynamic events such as large-scale environmental perturbations. Ignoring such temporal signals could give misleading information about stock structure. A single homogenous stock of *P. leopardus* may have been suggested if otolith structure based on the 1999 PCA results alone were considered, whereas two potential stocks would be inferred from both the PCA and CDA analyses of the 1995 data (Figs. 2A; 5A). In addition, cohorts were distinguishable within all regions based on the frequency distributions of DF scores. Other investigations of the interannual stability in otolith morphology of marine fishes have found differences between years, as well as age groups (Castonguay et al., 1991; Campana and Casselman, 1993; Begg and Brown, 2000; Begg et al., 2001). Consequently, when using otolith morphology to investigate stock structure, it is preferable to compare multiple cohorts with individuals of the same age, collected over several years. Such a sampling design would minimize confounding spatial variation in otolith shape with particular times of sampling and derive a time-averaged assessment of the spatial structure of a stock.

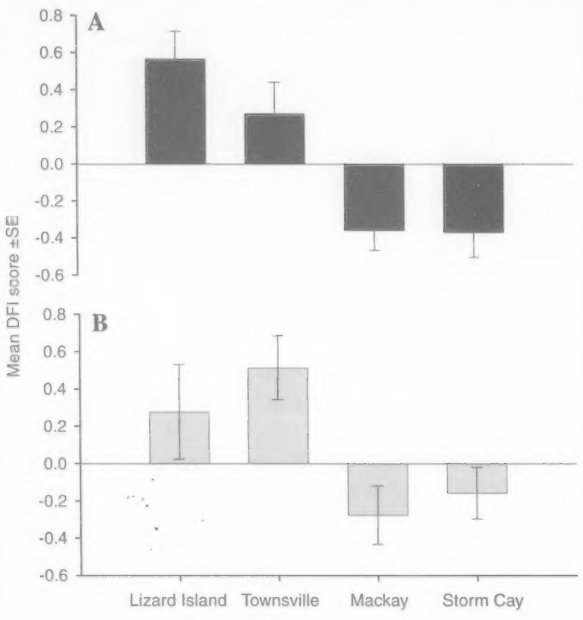

Figure 5

Mean ±SE of discriminant function (DF) I scores from otolith morphological variables (Fourier harmonics and shape variables combined) per region for (A) cohort 1995, and (B) cohort 1999 in four-year-old common coral trout (*Plectropomus leopardus*) from the Great Barrier Reef. (The data were pooled across reefs within regions.)

The spatial and temporal patterns in otolith shape are in part consistent with the assessment (based on otolith microchemistry) of stock structure of *P. leopardus* on the Great Barrier Reef (Bergenius et al., 2005). Differences in otolith chemistry of *P. leopardus* collected at the same spatial and temporal scales as those considered in this study have indicated the presence of two or three regional stocks. Thus, although the number and potential boundaries of phenotypic stocks based on otolith chemistry and otolith structure remain uncertain, the combined results of these studies emphasize the potential presence of several stocks of *P. leopardus* on the GBR and indicate a north-south demarcation. Differences in both otolith

Table 7

Canonical coefficient function representing correlation between the morphological variables (Fourier harmonics and shape variables combined) and significant discriminant functions (DFs), separating two cohorts (1995 and 1999) of four-year-old *Plectropomus leopardus* within each of four regions of the Great Barrier Reef. All variables selected in the models are shown, but variables with loadings <0.45 are not interpreted further.

Variable	Lizard Island DF I	Townsville DF I	Mackay DF I	Storm Cay DF I	1995 DF I	1995 DF II	1999 DF I
Log_{10} area			−0.62		0.59	−0.37	
Rectangularity				0.38			
Log_{10} circularity		−0.58					1
Sqrt harmonic 9		0.49	0.57				
Sqrt harmonic 114				0.62			
Sqrt harmonic 115	−0.24						
Sqrt harmonic 118	0.84				−0.46	0.23	
Sqrt harmonic 123			0.35				
Sqrt harmonic 124		0.22		0.49	0.45	0.52	
Sqrt harmonic 125			0.41		−0.12	0.69	

Table 8

Correctly classified individuals of four-year-old *Plectropomus leopardus* per cohort (1995 and 1999) in each of four regions of the Great Barrier Reef.

Cohort	Lizard Island	Townsville	Mackay	Storm Cay
1995	63.79	71.43	78.33	76.79
1999	73.91	83.33	70.45	63.64
Total	66.70	76.30	75.00	71.00

Table 9

Correctly classified individuals of four year old *Plectropomus leopardus* per region on the GBR in each of two cohorts (1995 and 1999).

Region	1995	1999
Lizard Island	39.66	17.39
Townsville	28.57	58.33
Mackay	45.00	53.49
Storm Cay	41.07	11.36
Total	39.70	34.30

shape and chemistry indicated that the movements of adults of *P. leopardus* may be limited and are consistent with the presumed sedentary (reef-specific) habit of most serranids after settlement (e.g., Chapman and Kramer, 2000; Stewart and Jones, 2001). Our results confirm those of several tagging studies of *P. leopardus* on the GBR which showed that individuals are unlikely to move among reefs after settlement (Davies, 1995; Zeller, 1998; Zeller and Russ, 1998). Such limited inter-stock movement of adults means that the recovery rate of stocks after significant harvest is largely (if not solely) dependent on some unknown level of larval dispersal. Further investigations, therefore, are required to clarify the implications of this potential stock structure of *P. leopardus* to ensure sustainable harvests at the appropriate scale for both management and the stock structure of the fish.

Reasons for temporal and spatial variation in otolith structure

Little is known about what processes influence the expression of traits responsible for otolith shape (Ihssen et al., 1981). Differences in growth rate has been the main reason given for differences in linear morphological variables of otoliths (e.g., Reznick et al., 1989; Secor and Dean, 1989; Begg et al., 2001), as well as outline shape variables (e.g., Castonguay et al., 1991; Smith, 1992; Campana and Casselman, 1993; Begg and Brown, 2000). In our study, *P. leopardus* subsamples were restricted to a certain size range to minimize the potential of a growth rate effect that could confound spatial or cohort related differences in otolith shape. Significant differences in growth rates (indicated by mean FL of four-year-olds), however, were apparent among reefs within regions in the complete sample from the ELF experiment (Bergenius et al.[8]), whereas there was no consistency in the patterns of variation in FL and any of the otolith morphological variables. It is possible that the large variation in FL among reefs could have masked potential differences in broad-scale regional differences in growth rates, or that some other developmental rate, such as maturation or reproductive output, were more important in influencing the otolith shape of *P. leopardus*.

Spatial and temporal variability in otolith shape would be expected in *P. leopardus* populations along the GBR given the natural variability in biological and hydrodynamic factors between reefs and regions (Wolanski, 1994), which in turn could affect various fish developmental rates. There was no monotonic latitudinal trend apparent in any of the otolith morphological variables related to a temperature gradient. The maximum difference in monthly average sea surface temperature among the latitudes examined in our study is typically less than 2°C (Lough, 1994). In contrast, there is regional (broad spatial scale) variability in the upwelling and inflow of cool nutrient rich oceanic water across the continental shelf of the GBR (e.g., Andrews and Gentien, 1982; Andrews, 1983; Wolanski, 1994; Middleton et al., 1995) which could potentially influence fish developmental rates through changes in food availability or "step-wise" patterns in water temperature.

There is also a possibility that the temporal variability in otolith shape of *P. leopardus* collected before and after Cyclone Justin in 1997 was related to associated temperature or other climatic changes. Cyclone Justin was an unusually large cyclone that remained in the Coral Sea adjacent to the GBR for over three weeks during March 1997. It caused a large and rapid drop in water temperature over the southern half of the GBR (south of ~17–18°S) during this time, and bottom water temperatures dropped in just one month (March) to below the average winter minimum not usually reached until July (AIMS[5]). Our study revealed a significant difference in otolith shape between nonoverlapping cohorts sampled in 1995 and 1999 in the Mackay region, which is one of the regions where the temperature changes would have been greatest.

Management and future directions

Although differences in otolith shape of *P. leopardus* may give an indication of stock structure, an examination of the relevance of these patterns for fisheries management should be the next step. A recent increase in the total

[8] Bergenius M. A. J., B. D. Mapstone, G. R. Russ, and G. A. Begg. 2005. Unpubl. data from the Effects of line fishing experiment (Mapstone et al., 2004). CRC Reef Research Centre, Townsville, Australia. [Data are on files at the CRC Reef Research Centre, James Cook University, Townsville, Queensland 4810, Australia.]

area of the GBR Marine Park (designated as marine national park zones [or no-take zones]) from about 5% to 33% enhances the potential for displacement of fishing effort between regions. If the proposed stocks have different life history characteristics and, potentially, different fishery productivities, less productive stocks may be subjected to greater harvest levels and increased risk of local depletion. Information on vital life history characteristics (e.g., growth, mortality, and maturity) is therefore needed to examine the potential impacts of fishing and related harvest strategies for the postulated stocks. Moreover, until more is known about how larvae relate between stocks, prudent and precautionary management should recognize groups of fish that function as individual units or stocks in response to harvest and management (Haddon and Willis, 1995).

Otoliths are often collected during routine sampling undertaken as part of the monitoring procedures and assessments of exploited fish stocks. As a result there may be large archives of otoliths available for morphological analyses in most fisheries laboratories. We therefore suggest that patterns in otolith morphology provide a cost and time effective starting point for directing further research on groups of harvested coral reef fishes that have lived at least parts of their life in different environments.

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Biological characteristics and mortality of western butterfish (*Pentapodus vitta*), an abundant bycatch species of prawn trawling and recreational fishing in a large subtropical embayment

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Abstract—The western butterfish (*Pentapodus vitta*) is numerous in the bycatch of prawn trawling and recreational fishing in Shark Bay, Western Australia. We have thus determined crucial aspects of its biological characteristics and the potential impact of fishing on its abundance within this large subtropical marine embayment. Although both sexes attained a maximum age of 8 years, males grow more rapidly and to a larger size. Maturity is attained at the end of the first year of life and spawning occurs between October and January. The use of a Bayesian approach to combine independent estimates for total mortality, Z, and natural mortality, M, yielded slightly higher point estimates for Z than M. This result indicates that *P. vitta* is lightly impacted by fishing. It is relevant that, potentially, the individuals can spawn twice before recruitment into the fishery and that 73% of recreationally caught individuals are returned live to the water.

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The family Nemipteridae (threadfin breams) is found in tropical and subtropical waters of the Indo-west Pacific (Nelson, 1994). The western butterfish (*Pentapodus vitta*) (also known as "striped whiptail"[1]) is a small benthic nemipterid, which is endemic to Western Australia (Russell, 1990) and very numerous in Shark Bay on the west coast of this state (Heithaus, 2004). It is also very abundant in the bycatch of the prawn trawl and recreational fisheries in this large subtropical environment. However, as with the vast majority of bycatch species in embayments, no estimate has been made of the mortality of *P. vitta* due to fishing. Furthermore, although *P. vitta* is very abundant in certain environments, there are no data on the age composition, growth, and reproductive biology based on validated age data for a population of this species. Indeed, previous studies of the Nemipteridae have focused almost entirely on species of *Nemipteris* and *Scolopsis*, which are widely distributed throughout the Indo-Pacific, where they are an important component of commercial and artisinal fisheries (Sainsbury and Whitelaw, 1984; Young and Martin, 1985; Murty et al., 1992; Zacharia, 1998).

The present study elucidates key aspects of the biology of *P. vitta* and, in particular, length-weight relationships, size and age compositions, growth, size and age at maturity, duration of the spawning period, and mortality. Focus is also placed on ascertaining whether this species is hermaphroditic, as is the case with certain other nemipterids (Young and Martin, 1985). The question of whether the mortality of a species with the "characteristics" of *P. vitta* is particularly attributable to sub-

[1] FishBase. http://www.fishbase.org/search.php [accessed June 2006].

stantial trawling and recreational fishing in an embayment has also been explored. For this purpose, we have used a model that reconciles the often imprecise and conflicting estimates of total and natural mortality that are obtained by using traditional approaches (Hall et al., 2004).

Materials and methods

Sampling regime

766 *P. vitta*, ranging from 90 to 198 mm in fork length (FL), were collected by trawling throughout Shark Bay in November and December 1997. Trawling was conducted at night by using twin 11-m prawn trawl nets with 50-mm mesh in the panels and 44-mm mesh in the codends, as are employed by commercial prawn trawl operators in Shark Bay. Each trawl lasted 20 minutes. The samples collected were used for estimating the mortality of western butterfish in Shark Bay. *Pentapodus vitta* (n=339), ranging from 31 to 215 mm in fork length, were also collected in many months from 1999 to 2004 by using trawls, hook-and-line fishing, and beach seines. These samples were used to obtain aging, growth, and reproductive data in the study.

Relationships of total length and weight to fork length

The fork length (FL) of each fish, and the total length (TL) of each fish whose caudal fin was not damaged, were measured to the nearest 1 mm. The relationship between TL and FL of each sex was then calculated by using the equation

$$TL = a + b \times FL,$$

to enable the TL of any fish with a damaged caudal fin to be estimated from its FL. The weight of each fish (W) was recorded to the nearest 1 g. The relationships between the fork length and weight of females and males were described by the equation

$$\log W = \log a + b \log FL.$$

Analysis of covariance (ANCOVA, α=0.05) was used to determine whether the relationships between TL and FL and between weight and FL of the males and females of *P. vitta* were significantly different (Zar, 1999).

Validation of the aging method and age determination

The sagittal otoliths of each *P. vitta* were removed, cleaned, and stored in labelled paper envelopes. Because a preliminary examination demonstrated that the growth zones were often easier to discern in sectioned than in whole otoliths, all fish were aged by using sectioned otoliths. Transverse sections of each otolith, 0.3–0.5 mm thick, were cut through the primordium by using a low-speed jewellery saw and then ground using 9-μm lapping film. These sections were then mounted on glass slides and viewed with transmitted light under a dissecting microscope.

Validation that a single growth zone is formed each year in otoliths of *P. vitta* was undertaken by using marginal increment analysis. The distance between the outer edge of the outermost opaque zone and the periphery of the otolith section (the marginal increment) was measured on the sectioned otoliths of each fish caught between June 1999 and May 2000. The marginal increment was then expressed either as a proportion of the distance between the primordium and the outer edge of the opaque zone, when only one opaque zone was present, or as a proportion of the distance between the outer edges of the two outermost opaque zones, when two or more opaque zones were present. All measurements were made with the Leica Image Manager 1000 (Leica Microsystems AG, Wetzlar, Germany).

Ages were assigned to each *P. vitta* on the basis of the number of opaque zones (annuli) in sectioned otoliths and by taking into account the dates of capture and the birth date of the fish. The birth date was designated as 1 December because this date corresponded approximately to the mid-point of the period when, on the basis of gonadosomatic indices and the trends shown by gonadal and oocyte development, *P. vitta* spawn (see "Discussion" section). The opaque zones were counted in the region between the primordium and the proximal surface along the ventral and dorsal margins of the sulcus acousticus, where the opaque bands were usually well defined and thus easily identified. The opaque zones in each otolith were counted without knowledge of the length or date of capture of the fish from which that otolith had come.

The precision of the counts from 175 *P. vitta* otolith sections made by the senior author (JCM) on two separate occasions and between JCM's second count and a count made by another experienced reader, was assessed by using the index average percent error (IAPE) of Beamish and Fournier (1981). The IAPE values were low (i.e., 0.7%) for the two counts made by the senior author (JCM)) and for JCM's second count and that of the independent reader (i.e., 3.9%), demonstrating a high level of precision for the otolith readings. Because the senior author was more experienced in reading the otoliths of *P. vitta*, his second round of counts (and these were almost invariably the same as in the first round of counts) was used for determining the ages of individual fish.

Growth

Fish caught by all methods in all months (except those obtained during extensive trawling in November and December 1997)—fish that collectively covered the full size range of *P. vitta*, were used to provide data for constructing growth curves. The large samples collected by trawling in November and December 1997 were excluded because they would have introduced an excessive bias towards the larger fish at younger ages (see Ricker

[1975] for importance of limiting bias by using data from multiple sampling methods). Von Bertalanffy growth equations were fitted to the fork lengths of the female and male fish at their estimated ages at capture by using nonlinear regression in the Statistical Package for the Social Sciences software (SPSS 12.0.2 for Windows, SPSS Inc., Chicago, IL). The lengths at age of small fish whose sex could not be determined were allocated randomly to both the male and female data sets used for calculating the growth curves. The von Bertalanffy growth equation is

$$L_t = L_\infty(1 - \exp^{-k(t-t_0)}).$$

where L_t = the estimated length at age t;
L_∞ = the asymptotic length;
k = the rate at which L_t approaches L_∞; and
t_0 = the hypothetical age at zero length.

A likelihood-ratio test was used to compare the growth curves of the females and males of *P. vitta* (Cerrato, 1990). The hypothesis that a common growth curve could be fitted for the two sexes was rejected at the $\alpha = 0.05$ level of significance if the test statistic, calculated as twice the difference between the log-likelihoods obtained by fitting a common growth curve for both sexes and by fitting separate growth curves for each sex, exceeded $\chi^2_\alpha(q)$, where q is the difference between the numbers of parameters (i.e., 3) in the two approaches.

Reproductive biology

The gonads of each fish that could be sexed macroscopically were removed and weighed to the nearest 0.01 g and, in the case of ovaries, staged macroscopically by using the scheme of Laevastu (1965) and the histological characteristics of the ovaries. For histology, ovaries of a random subsample of female *P. vitta* from each month of the year were preserved in Bouin's fixative for 48 hours, after which they were dehydrated in an ascending series of alcohol concentrations, embedded in paraffin wax, cut into 6-μm thick sections, and stained with either Ehrlich's haematoxylin and eosin or Mallory's trichrome (Humanson, 1972). On each histological slide, the maximum and minimum diameters of 30 randomly selected oocytes, which had been sectioned through their nuclei, were recorded to the nearest 5 μm. The mean of these two measurements for each oocyte was considered to represent the diameter of that oocyte (see Foucher and Beamish, 1980).

The gonadosomatic indices (GSIs) of females and males ≥1 year of age were determined from the equation

$$W1/W2 \times 100,$$

where $W1$ = weight of gonad; and
$W2$ = weight of whole fish minus the weight of gonad.

Mortality

Age-frequency distributions for female and male *P. vitta* caught during extensive trawling in November and December 1997 were used to estimate the instantaneous rate of total mortality (Z) for both females and males. Age classes on the descending limb of the age-frequency distribution for each sex (i.e., immediately after the peak in this distribution), were considered fully recruited to the fishery (Ricker, 1975). The catch curve for each sex was analysed by using the assumptions that Z and the levels of annual recruitment are constant and that the age composition of fully recruited fish represents a random sample from a multinominal distribution with uniform selectivity from the age of full recruitment (Hall et al., 2004). The value of Z was estimated by maximizing the log-likelihood by using the SOLVER routine in Microsoft™ Excel (vers. 2002, Microsoft Inc., Redmond, WA). The data for *P. vitta* were randomly resampled with replacement and analyzed to create 1000 sets of bootstrap estimates. The point estimate for Z was taken as the median of the 1000 bootstrap estimates. The 95% confidence limits were calculated as the 2.5 and 97.5 percentiles of the corresponding estimated values. The likelihood-ratio test used to compare growth curves was also used to compare the catch curves for the two sexes.

Estimates of natural mortality, M, for female and male *P. vitta* were calculated from the relationship between natural mortality, growth, and water temperature (Pauly, 1980). This relationship was refitted to Pauly's data for 175 fish stocks by using SPSS 12.0.2 for Windows (SPSS Inc., Chicago, IL). The values of k (per year) and L_∞ (cm TL), estimated from the asymptotic FL in the growth curves derived for *P. vitta*, and the water temperature, T, were then inserted into SPSS to obtain point estimates and associated 95% confidence limits for M, thereby taking into account the uncertainty of the parameter estimates and the variation of the data around the regression line. The mean annual bottom water temperature in Shark Bay is 23.1°C (data provided by Department of Fisheries Western Australia).

The values for mortality, derived for each sex by using the above approaches, were combined with the estimates of total mortality obtained from the maximum recorded ages of the two sexes with Hoenig's (1983) regression model for fish and those obtained with a simulation approach (Hall et al., 2004). This method reconciles the inconsistencies among the individual estimates of mortality and, through combining the different values, improves the precision of the resulting estimates of natural and total mortality. To provide a more precise estimate, the simulation routine was modified slightly from that described by Hall et al. (2004) to use the number of males or females within the sample that were older than a specified age rather than the age associated with the oldest of those fish.

Results

Relationships of total length and weight to fork length

The relationships between the FL and TL of females and males, which covered essentially the full size range of *P. vitta*, did not differ significantly ($P>0.05$) and therefore the length data for the two sexes were pooled. The linear relationship between FL and TL for both sexes of *P. vitta* combined is described by the equation

$$TL = -2.35 + 1.12\,FL \qquad (n=344,\ r^2=0.99).$$

Moreover, because the relationship between weight and fork length of western butterfish did not differ significantly between males and females ($P>0.05$), these data for the two sexes were pooled. The relationship between weight and fork length for both sexes combined was described by the equation

$$\log W = \log 1.22x\ 10^{-5} + 3.06 \log FL \quad (n=1026,\ r^2=0.99).$$

Validation of aging method

The mean monthly marginal increments on sectioned otoliths of western butterfish with one, two, three, and four–seven opaque zones reached their maxima in October, after which they declined markedly to their minima in either November or December and then rose progressively over the ensuing months (Fig. 1). The pronounced decline and then progressive rise, exhibited by the mean monthly marginal increments on the otoliths of western butterfish, irrespective of the number of opaque zones, demonstrates that a single opaque zone is formed in the otoliths of *P. vitta* each year and that the number of such zones can thus be used to age this species accurately.

Growth

The von Bertalanffy growth curve provided a good fit to the fork lengths at age of the females and males of *P. vitta* (Fig. 2). This good fit is reflected in the high coefficients of determination (r^2) of 0.942 for females and 0.924 for males and by the values for t_0 being close to zero (Table 1). The von Bertalanffy growth curves of the females and males of *P. vitta* in Shark Bay differed significantly ($P<0.05$), and the difference in L_∞ between females and males contributed more to the difference than that of either k or t_0.

Females were more prevalent than males in length classes below 160 mm, whereas the opposite was true above this length (Fig. 3A). However, age-frequency distributions showed that females were more prevalent in all age classes (Fig. 3B). The overall sex ratio was 1.4 females:1 male.

Reproductive biology

Because virtually all *P. vitta* became mature at the end of their first year of life, the GSIs for all fish ≥1 year of age were calculated. The mean monthly GSIs for female western butterfish remained low (<0.9) in winter (June to August) and early spring (September), but then increased sharply from September to reach a maximum of 4.0 in late spring (November), before declining markedly during mid-summer (January) (Fig. 4). Although the pronounced seasonal trend displayed by the mean monthly GSIs for males was very similar to that for females, the maximum mean monthly GSI of males was approximately one tenth of that for females.

All female western butterfish that were ≥1 year old and caught between February and August (apart from a few in July) possessed ovaries at stage I or II (i.e., they were virgin or immature; Fig. 5). Females with

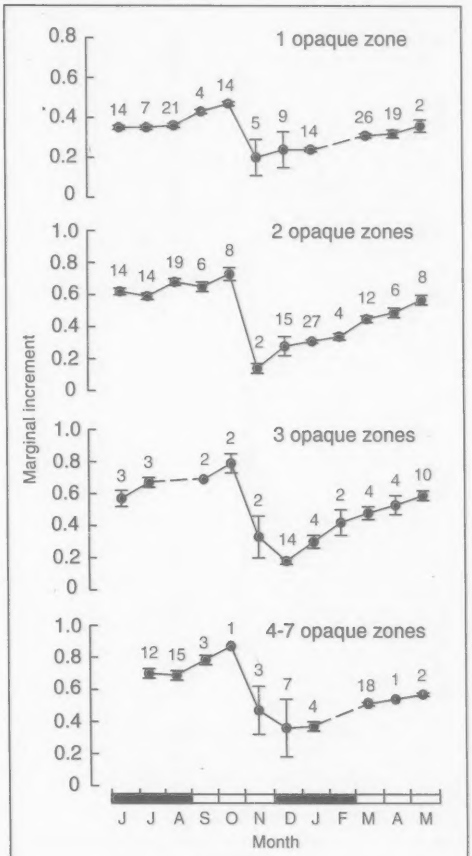

Figure 1

Mean monthly marginal increments (±1 standard error) for sagittal otoliths of the western butterfish (*Pentapodus vitta*), derived from samples collected between 1999 and 2004. Sample size is given for each month. The closed rectangles represent the summer and winter months and the open rectangles the autumn and spring months.

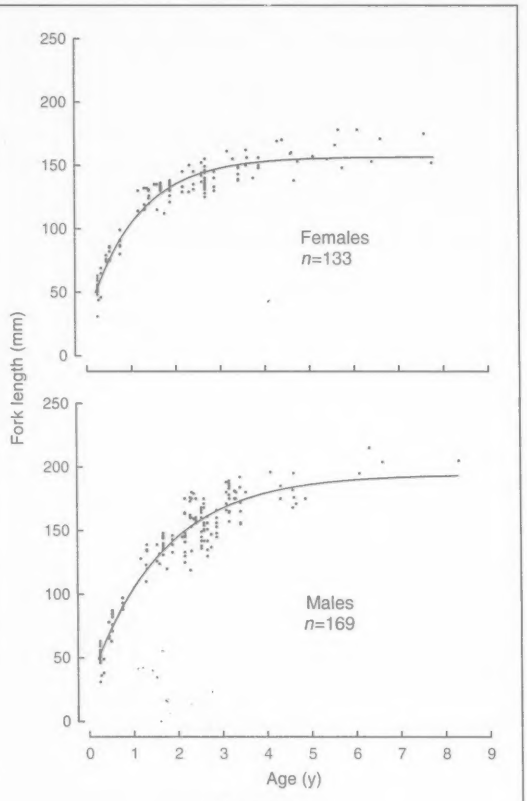

Figure 2

Von Bertalanffy growth curves fitted to fork lengths at age for individual females and males of western butterfish (*Pentapodus vitta*).

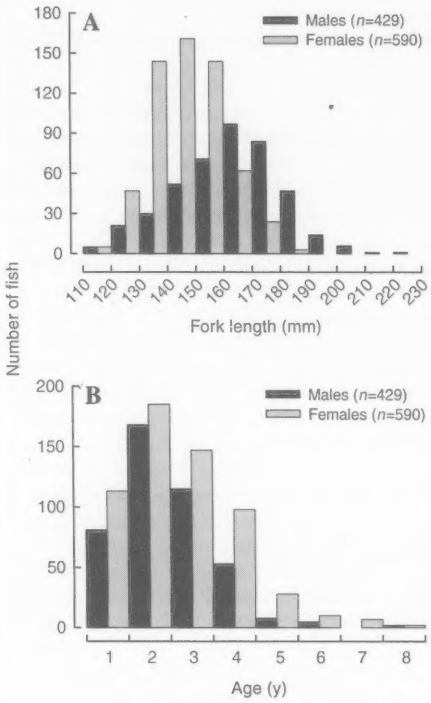

Figure 3

(**A**) Length-frequency and (**B**) age-frequency distributions for males and females of western butterfish (*Pentapodus vitta*).

Table 1

Von Bertalanffy growth parameters and their upper and lower 95% confidence limits for females and males of the western butterfish (*Pentapodus vitta*) in Shark Bay. r^2= coefficient of determination; n=number of fish in sample.

Sex	Confidence intervals	k (/year)	L_∞ (mm FL)	t_0 (years)	r^2	n
Females	Estimate	0.886	156.6	−0.233	0.942	133
	Upper	0.928	159.2	−0.058		
	Lower	0.844	154.0	−0.408		
Males	Estimate	0.602	194.4	−0.282	0.924	169
	Upper	0.624	197.9	−0.189		
	Lower	0.580	190.9	−0.375		

stage-III (developing) and stage-IV (maturing) ovaries were first found in July and were also present in September. Fish with stage-V (prespawning) and stage-VI (spawning) ovaries collectively dominated the samples obtained in October to December and were still the most prevalent group in January. The samples in January also contained one fish with stage-VIII (recovering spent) and some with stage-II ovaries but none with ovaries at stages III or IV (Fig. 5). The above trends provide strong evidence that any female with ovaries

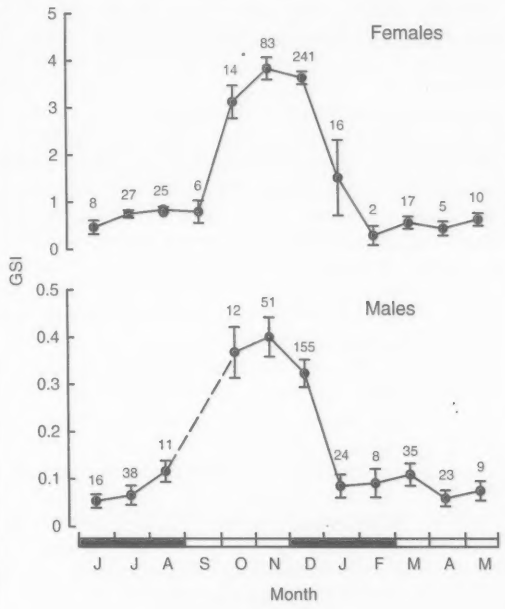

Figure 4

Mean monthly gonadosomatic indices (GSI) (±1 standard error) for females and males of western butterfish (*Pentapodus vitta*) that were ≥1 year old. Monthly sample sizes are given above each mean.

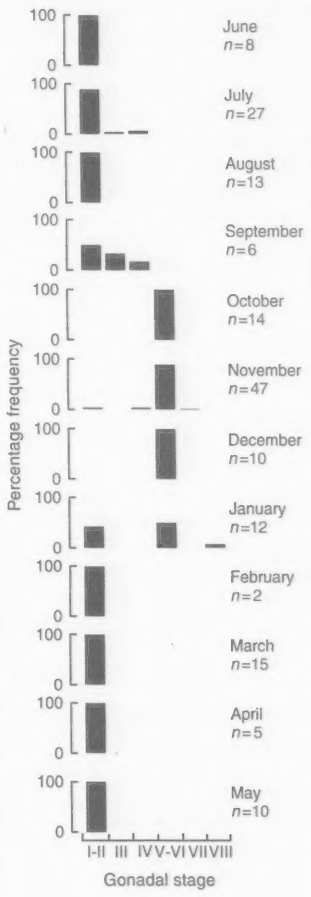

Figure 5

Histograms showing percent frequency of occurrence of each of the various gonadal stages in female western butterfish (*Pentapodus vitta*) in each month of the year.

that had developed to at least stage III by September would have progressed through to maturity during the ensuing months of the spawning period if it had not been removed from the population.

In each month, the distribution of oocyte diameters in the mature ovaries of *P. vitta* produced a well-defined mode between ~20 and 80 μm, which represented chromatin nucleolar- and perinucleolar-stage oocytes. Cortical alveolar oocytes were present in some ovaries in July and September, when oocyte diameters had reached a maximum of 200 and 150 μm, respectively. These larger oocytes and also yolk granule oocytes were abundant between October and December and reached a maximum diameter of 380 μm. The contribution of cortical alveolar and yolk granule oocytes declined in January. Hydrated oocytes were found in several ovaries in October, December, and January and postovulatory follicles were present in some ovaries during November.

Mortality

The age-frequency distributions for both female and male western butterfish caught during extensive trawling in November and December of 1997 had a modal peak at 2 years of age (Fig. 3B). Because the age at full recruitment was thus considered to be 3 years, catch curve analysis was undertaken with data for the 3+ and older age classes. The resulting point estimate for the instantaneous rate of total mortality, Z, was significantly greater ($P<0.05$) for males (1.15/year) than for females (0.91/year) (Table 2). Likewise, the simulation method of Hall et al. (2004), based on the number of individuals above 5 years of age (2 males and 13 females for sample sizes of 130 and 253, respectively), yielded a greater point estimate of Z for males (1.34/year) than females (0.89/year). The point estimate for Z, derived by inserting the maximum ages for female and male butterfish (8 years for both males and females), into the refitted Hoenig (1983) equation for fish, was 0.55/year for the two sexes (Table 2). The point estimates for the

instantaneous rate of natural mortality, M, derived by inserting the parameter values for western butterfish into the refitted Pauly (1980) equation, were higher for females (1.78/year) than males (1.28/year).

The combined point estimate for Z derived using the method of Hall et al. (2004) was greater for males (1.14/year) than females (0.89/year; Fig. 6). This method yielded a slightly higher point estimate of M for males (0.80/year) than females (0.71/year) (Fig. 6).

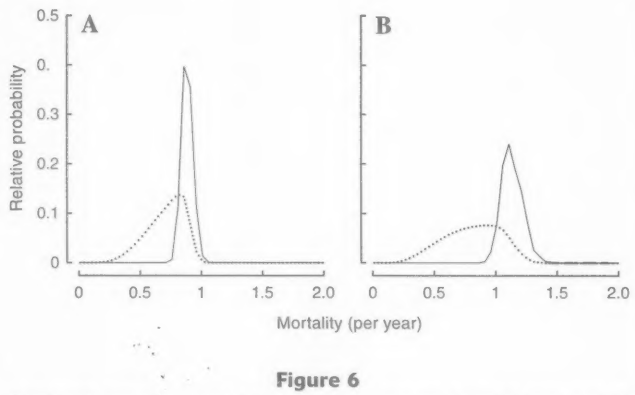

Figure 6

Combined posterior probability distributions for Z (solid line) and M (dotted line) for (**A**) females and (**B**) male western butterfish (*Pentapodus vitta*).

Discussion

Validation of aging method, age composition, and growth

The validation that the opaque zones of *P. vitta* are formed annually, together with the very high repeatability of their counts in sectioned otoliths, demonstrate that the number of these opaque zones (annuli) in sectioned otoliths can be reliably used for aging this nemipterid. Stephenson and Hall (2003) demonstrated that the annuli in sectioned otoliths of another nemipterid, *Nemipterus furcosus*, in Western Australia are also formed annually.

The vast majority of the *P. vitta* caught in Shark Bay were less than seven years old and the oldest individual was just over eight years old. The pattern of growth for females and males differed. Thus, the males of each age were, on average, larger than females after the first year of life and had a greater L_∞. However, most of the growth of both sexes occurs during the first three years of life.

Spawning period

The highly elevated mean monthly GSIs of females and males between October and December and the restriction of females with mature ovaries to the period between

Table 2

Point estimates and their 95% confidence intervals for total mortality, Z, and natural mortality, M, for the western butterfish (*Pentapodus vitta*), calculated by using life history models, estimation of longevity based on simulation, catch curve analysis and Bayesian analysis. Methods used for main interpretations of mortality are in bold.

Method of analysis	Z or M (/year)	Point estimate	Lower 95% CI	Upper 95% CI
Males				
Catch curve analysis	Z	1.15	0.96	1.33
Simulation (number of fish >5 years old)	Z	1.34	0.90	1.95
Refitted Hoenig (1983) fish equation	Z	0.55	0.19	1.52
Combined Z (Bayesian method)	**Z**	**1.14**	**1.01**	**1.35**
Refitted Pauly (1980)	M	1.28	0.42	3.91
Combined M (Bayesian method)	**M**	**0.80**	**0.37**	**1.23**
Females				
Catch curve analysis	Z	0.91	0.78	0.99
Simulation (number of fish >5 years old)	Z	0.89	0.69	1.11
Refitted Hoenig (1983) fish equation	Z	0.55	0.19	1.52
Combined Z (Bayesian method)	**Z**	**0.89**	**0.82**	**1.01**
Refitted Pauly (1980)	M	1.78	0.56	5.35
Combined M (Bayesian method)	**M**	**0.71**	**0.39**	**0.97**

October and January implies that *P. vitta* spawns during these latter four months. This conclusion is consistent with hydrated oocytes or postovulatory follicles or a combination of both being found only in fish caught between October and January. Furthermore, the precipitous decline in the mean monthly GSIs between December and February and the presence of only stage-II ovaries in February strongly indicates that spawning does not extend into this month. Because spawning activity peaked between October and January, the western butterfish was given a birth date of 1 December when an age was assigned to each fish. Because mature ovaries of *P. vitta* often contained a relatively wide size range of vitellogenic oocytes and, in many cases, also either hydrated oocytes or postovulatory follicles, this species is considered a multiple spawner *sensu* deVlaming (1983), namely individual females release eggs on more than one occasion in a spawning season.

Is there evidence that *Pentapodus vitta* is hermaphroditic?

Our data demonstrate that, in the population of *P. vitta* in Shark Bay, the females are relatively more abundant than males in length classes below 160 mm, whereas the reverse is true of length classes above that length (Fig. 3A). In contrast, the prevalence of females was always greater than that of males in each age class. The trend towards an increasing prevalence of males vs. females with increasing body length can thus be attributed to the males growing faster. The fact that there was not a progressive shift towards an increase in one sex with increasing age and none of the gonads of the 178 fish examined contained both ovarian and testicular tissue provides overwhelming circumstantial evidence that *P. vitta* is gonochoristic. Like *P. vitta*, other nemipterid species also exhibit a size-related skew in their sex ratios that can be explained by differences in growth rates between the two sexes (e.g., Young and Martin, 1985; Lau and Sadovy, 2001; Raje, 2002; Granada et al., 2004). The trend among gonochoristic nemipterids, for their males to grow larger than their females, presumably reflects a selective advantage of being large during courtship or mating (Granada et al., 2004). In contrast to these gonochoristic species, some nemipterids are protogynous hermaphrodites, e.g., *Scolopsis monogramma, S. taeniopterus* and *S. bilineatus* (Young and Martin, 1985).

Mortality

The point estimates for natural mortality, *M*, derived for males and females of *P. vitta* with Pauly's (1980) equation, were inconsistent with the point estimates derived for total mortality, *Z*. This conclusion is drawn from the fact that the point estimates for *M* were greater than those for *Z* from both Hoenig's (1983) equation for fish and catch curve analysis, thereby paralleling the situation with several other species (see Hall et al., 2004), and also those derived from the simulation and Bayesian methods of Hall et al. (2004). The use of the method of Hall et al. (2004) reconciled the inconsistencies between *M* and *Z* for *P. vitta* and provided more precise estimates, particularly for *M*. Because the point estimates for *Z* were only slightly greater than those for *M*, the population of *P. vitta* in Shark Bay does not appear to have been subjected to heavy fishing pressure. In this context, it is relevant that, because the vast majority of *P. vitta* attain maturity by the end of their first year of life, most individuals will have had the opportunity to spawn at least twice before they become fully recruited into the trawl fishery. Furthermore, recreational anglers return about 73% about of the western butterfish they catch in Shark Bay live to the water (Sumner et al.[2]).

Pentapodus vitta lives for up to eight years, but grows very rapidly early in life and attains maturity by the end of the first year of life. The males of *P. vitta* grow more rapidly and reach a larger size than their females. The western butterfish is a gonochoristic species that, in Shark Bay, spawns between mid-spring and mid-summer. Although commercial and recreational fishermen obtain large numbers of *P. vitta* as bycatch in Shark Bay, this fishing does not appear to have a marked impact on the numbers of this very abundant species in this large subtropical embayment.

Acknowledgments

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The use of multibeam sonar mapping techniques to refine population estimates of the endangered white abalone (*Haliotis sorenseni*)

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Abstract—Multibeam sonar mapping techniques provide detailed benthic habitat information that can be combined with the data on species-specific habitat preferences to provide highly accurate calculations of populations in a particular area. The amount of suitable habitat available for the endangered white abalone (*Haliotis sorenseni*) was quantified to aid in obtaining an accurate estimate of the number of remaining individuals at two offshore banks and one island site off the coast of southern California. Habitat was mapped by using multibeam sonar survey techniques and categorized by using rugosity and topographic position analysis. Abalone densities were evaluated by using a remotely operated vehicle and video transect methods. The total amount of suitable habitat at these three sites was far greater than that previously estimated. Therefore, although present estimates of white abalone densities are several orders of magnitude lower than historic estimates, the total population is likely larger than previously reported because of the additional amount of habitat surveyed in this study.

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Accurate classification of habitat is important for examinations of the distribution and abundance of marine organisms. The potential complexity of species-habitat relationships is such that the use of a single parameter when trying to link species to specific areas has become obsolete. Multiple physical oceanographic parameters that link species to their habitat have proven to be useful, although they are not applicable to all types of marine organisms (Freeman and Rogers, 2003). The use of high-resolution multibeam sonar maps for classifying habitat has become a critical step in the process of estimating the distribution and abundance of marine animals that are known to be associated with particular habitat types. Because an increasing number of marine resources are in states of decline, information on the amount of habitat of specific types and qualities becomes crucial to making predictions for the purposes of fisheries management, and to aid in decisions concerning potential locations of marine protected areas (Kvitek et al.[1]; Iampietro et al., in press). For species in states of decline, protection of known critical habitat may be the only approach available to enhance survival of the species. Detailed habitat mapping provides a large amount of information on the benthic makeup of an area in a relatively short amount of time, and further processing of data with GIS (geographic information system) can produce accurate estimates of actual areas categorized by various physical parameters. These pieces of information, coupled with field surveys to obtain information on animal or plant habitat associations,

[1] Kvitek, R., P. Iampietro, C. Bretz, K. Thomas, S. Zurita, B. Jones, and E. Morris. 2004. Hydrographic data acquisition in support of MLPA and MLMA Implementation. California Department of Fish and Game Final Report P0170015, p. 1–74. Foundation of California State University Monterey Bay, 100 Campus Center, Seaside, CA 93955.

can allow for detailed and accurate estimates of abundance of marine organisms.

The white abalone (*Haliotis sorenseni*) is one of six abalone species (red, green, pink, pinto, black, and white) that have been exploited commercially on the west coast of North America. The species ranged historically from Morro Bay, California, USA, to Punta Rompiente, Baja California, Mexico (Geiger, 1999). Serial depletion of stocks of congeneric, relatively shallow-dwelling abalone species led to the exploitation of white abalone, the deepest living abalone species in the North Pacific (Karpov et al., 2000). During a ten-year period from 1969 to 1978, approximately 360,000 white abalone were harvested (Hobday et al., 2001). After 1978, the mandatory reporting of white abalone landings was no longer required, and although abalone fishing effort has remained high, there are (at present) no data on the numbers taken (Tegner, 1989).

In surveys conducted in the late 1990s in suitable habitat, very low numbers of white abalone were reported (Davis et al., 1996, 1998; Haaker et al.[2]; Hobday et al., 2001). Densities at many localities were less than 1 abalone/ha, and the entire population of white abalone was estimated at less than 3000 individuals (Hobday et al., 2001). Reproductive efforts of the remaining adults are believed to have been seriously hindered by potential Allee effects (Allee, 1931) because of low densities. Concern for the survival of the species prompted a status review and the white abalone was listed as an endangered species by the Department of Commerce on 29 May 2001 (Federal Register, 2001).

Postexploitation estimates of abundance and available white abalone habitat need revision because the spatial coverage of sampling in the 1980s and 1990s was limited in the case of determining abundance estimates and virtually nonexistent in the case of determining habitat classification (Lafferty et al., 2004). Accurate estimates of density and the amount of suitable habitat are critical for making informed decisions regarding how to prioritize recovery actions and where to focus population enhancement efforts. In addition, identification of the specific locations of white abalone in the wild will help both to focus efforts to protect areas where the species remain and to locate potential brood stocks for captive breeding. Information on the recruitment potential of the remaining individuals cannot be directly assessed, but an examination of the temporal trends in size distributions may be helpful in addressing questions of population viability and sustainability. The present study was conducted with recovery efforts in mind, and therefore included intensive sampling of offshore banks and islands where white abalone abundance was high historically. We used a combination of advanced mapping technology (multibeam sonar and side-scan sonar) and a remotely operated vehicle (ROV) to quantify the total amount of available habitat at each location, in order to examine the size distributions of surviving populations, and to derive new estimates of white abalone abundance.

Materials and methods

Habitat mapping

Habitat was surveyed during three cruises on the NOAA ship RV *David Starr Jordan* at Tanner Bank (July 2002 and September 2004), Cortes Bank (July 2003), and San Clemente Island (August 2004) with multibeam (all years, Fig.1) and side-scan sonar techniques (2002 only). The multibeam sonar system, which was installed on the RV *David Starr Jordan* for the Tanner Bank 2002 and Cortes Bank 2003 cruises, included a Reson 8101 multibeam sonar (Reson Inc. Goleta, CA) supplemented with a side-scan sonar option, and was used in conjunction with a Triton-Elics Isis System (Triton Elics International, Portland, OR) for data logging and sonar control. The San Clemente Island 2004 habitat survey was conducted by using the same sonar system aboard a smaller vessel, the RV *VenTresca*, in conjunction with ROV operations conducted aboard the RV *David Starr Jordan*. Delphmap and BathyPro software (Triton Elics International, Inc., Portland, OR) were used to create real-time side-scan mosaics and to generate digital elevation models. The pitch and roll motion of the vessel used for mapping was corrected for using a TSS HDMS (heading and dynamic motion sensor) (pitch, roll and heading accuracy ±0.02°; heave accuracy ±5% or 5 cm). Hypack Max software (Hypack, Inc., Middletown, CT) was used for survey planning and navigation. Positioning information was provided by a Trimble 4700 GPS receiver and NavBeacon for receiving U.S. Coast Guard RTCM (radio technical commission for maritime communications) corrections. Sound velocity profile data were collected with an Applied Microsystems (Sydney, British Columbia, and CA) SVPlus sound velocimeter. Multibeam data were processed with CARIS HIPS software (CARIS USA, Ellicott City, MD), and all final GIS products were derived from shoal-biased data.

Microhabitat analysis

Habitat type and algal cover were examined for surveys conducted at Tanner Bank in 2002. Habitat was characterized by broad type (e.g., bank, seamount), modifiers (e.g., faulted, eroded), microhabitat (e.g., sand, boulders), seafloor slope (by degree), seafloor complexity (5 levels), and algal cover (species identification and four levels of coverage), after Greene et al. (1999; Table 1).

Abalone surveys

Abalone surveys were conducted with a Phantom HD 2 + 2 (2002 and 2003) and a Phantom DS4 (2004)

[2] Haaker, P. L., D. V. Richards, and I. Tanaguchi. 2000. White abalone program October 9–25, 1999, cruise report, p. 1–17. California Department of Fish and Game, 330 Golden Shore Suite 50, Long Beach, CA 90802.

Table 1

Habitat analysis variable descriptions (Greene et al., 1999). Only those classifications that were used frequently enough to influence the PCA write out are listed (a total of 12 were included in the analysis). For algal levels, coverage was defined by the following within the video-captured field of view: absent = <10%, rare = 10–35%, present = 35–75%, and highly abundant = 75–100%.

Variable abbreviation	Variable type	Levels
Mhab 1–4	Macro/Microhabitat	1=boulders; 2=deformed (faulted or folded); 3=deformed (faulted or folded) + boulders; 4=deformed (faulted or folded) + sand
Slope 1 and 2	Seafloor slope	1=flat (0 to 1 degree); 2=sloping (1 to 30 degrees)
Com 1 and 2	Seafloor complexity	1=very low complexity; 2=low complexity
Br 1–4	All brown algae	1=absent; 2=rare; 3=present; 4=highly abundant
L 1–4	*Laminaria farlowii*	1=absent; 2=rare; 3=present; 4=highly abundant
A 1–4	*Agarum fimbriatum*	1=absent; 2=rare; 3=present; 4=highly abundant
E 1–4	*Eisenia arborea*	1=absent; 2=rare; 3=present; 4=highly abundant
D 1–4	*Dictyotaceae* spp.	1=absent; 2=rare; 3=present; 4=highly abundant

remotely operated vehicle (ROV) equipped with a forward-looking 12:1 zoom color video camera (all surveys) and a high resolution Nikon Coolpix digital still camera (2004 surveys only, Insite Pacific Inc., Solana Beach, CA). We recorded video footage continuously on digital tapes and overlaid footage with temperature, depth, heading, and time information from an on-screen display. Two pairs of lasers were mounted near the front of the ROV in parallel: one pair to measure abalone upon sighting (10.0 cm apart), and one pair to estimate the search field of view (60 cm apart). Upon sighting an abalone, the ROV pilot maneuvered the vehicle into position to zoom in on and photograph the animal for species confirmation, ensuring that the narrow pair of lasers passed over the abalone so that a size estimate could be obtained. Empty abalone shells were also noted and identified.

The ROV was tracked by using a directional hydrophone mounted on the ship and a transponder mounted on the ROV. Positional data and all other navigational and physical data associated with the ROV dives (e.g., heading, depth, and water temperature) were recorded every two seconds. Because of the great depth range that white abalone inhabit, it was not logistically feasible to compare ROV transect observations with diver transect observations. It is possible that we missed abalone residing on the back sides of rocks as the ROV passed over.

Sampling design and site selection

Multibeam and side-scan surveys were conducted the preceding night at sites that were to be surveyed with the ROV during the next day. Transect locations were chosen randomly initially, but after preliminary surveys at Tanner Bank revealed a narrow depth range of abalone occurrence from 30 to 60 m and a habitat restriction to rock reef or the sand-and-rock reef interface, only areas of suitable habitat (depths ranging from 30 to 60 m [±5 m]) were surveyed. In general, we attempted to run transects for approximately two hours, and to a length of 1 km, although actual lengths were calculated after the dive. Several of the early surveys included transects of greater lengths of time and distances. Georeferenced bathymetry maps were interfaced with the ROV navigational software for all dives, allowing for the ship, and in effect the ROV, to remain within a particular depth stratum and within suitable habitat.

Postdive processing

Videotapes and still photos were reviewed to confirm species identification, measure sizes, search for additional abalone, record search effort, examine microhabitat, and determine the search field of view. Other abalone species that were encountered were noted (red and pink). We used strip transect techniques to estimate densities, and therefore the field of view was measured for abalone sightings from the first survey (Tanner Bank, 2002), and the average (2 m [±0.85 SD], n=171) was used as the strip width for the entirety of each transect in the study.

Data analysis

For habitat classification a statistical approach called textural analysis (described in Cochrane and Lafferty, 2002) was used to identify complex rock areas at Tanner Bank as documented by side-scan sonar (Fig. 1, A and B). We estimated the total area of available white abalone habitat on each bank by calculating the amount of rocky substrate in depth intervals, as determined by multibeam sonar surveys. A combination of rugosity and topographic position analysis (TPI) were used

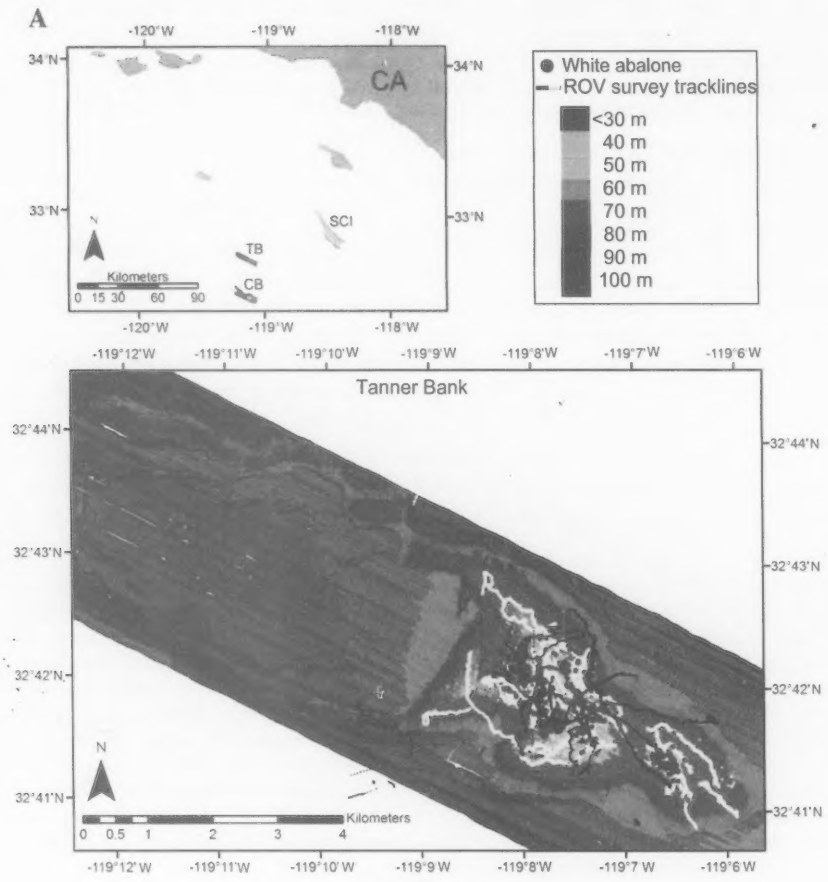

Figure 1

(**A**) High-resolution bathymetry of Tanner Bank and map of the southern California coast. Black lines represent ROV transect track lines in 2002 and yellow lines represent track lines in 2004. Pink dots on track lines represent white abalone (*Haliotis sorenseni*) sightings. Depth strata are distinguished by color (see legend). CA=California; SCI=San Clemente Island; TB=Tanner Bank; CB=Cortes Bank. (**B**) High-resolution bathymetry of Cortes Bank and San Clemente Island. Black lines represent ROV transect track lines. Pink dots on track lines represent white abalone (*Haliotis sorenseni*) sightings. Depth strata are distinguished by color (see legend).

for multibeam habitat classification (Kvitek et al.[3]). A rugosity measure was used to evaluate the "texture" of the seafloor by quantifying the surface area to planar area. Rugosity calculations were done with ArcView 3.2 (ESRI, Redlands, CA) by using the "Surface Area and Ratios from Elevation Grid , vers 1.2." (Jenness, 2002). Rugosity measures ranged from 1 to 4, and higher values indicated more texture (i.e., rocky terrain). TPI was calculated in ArcGIS, vers. 8.3 by a multistep process. For each cell the focal mean of the digital elevation model (DEM) was calculated to compute an average depth value used to obtain a measure of relative elevation. Relative elevations were classified into six TPI classes to allow for visual representation of elevations. Bottom types were noted during ROV surveys and compared to bottom types determined by sonar data, and in all cases results were confirmed.

Principal component analysis (PCA) was used to examine potential relationships between habitat type and

[3] Kvitek, R. G., P. J. Iampietro, and E. Summers-Morris. 2003. Integrated spatial data model tools set for the auto-classification and delineation of species-specific habitat maps from high-resolution, digital hydrographic data. Report prepared for NOAA National Ocean Service (NOS), p 1–74. NOAA Coastal Services Center, 2234 South Hobson Ave., Charleston, SC 29405.

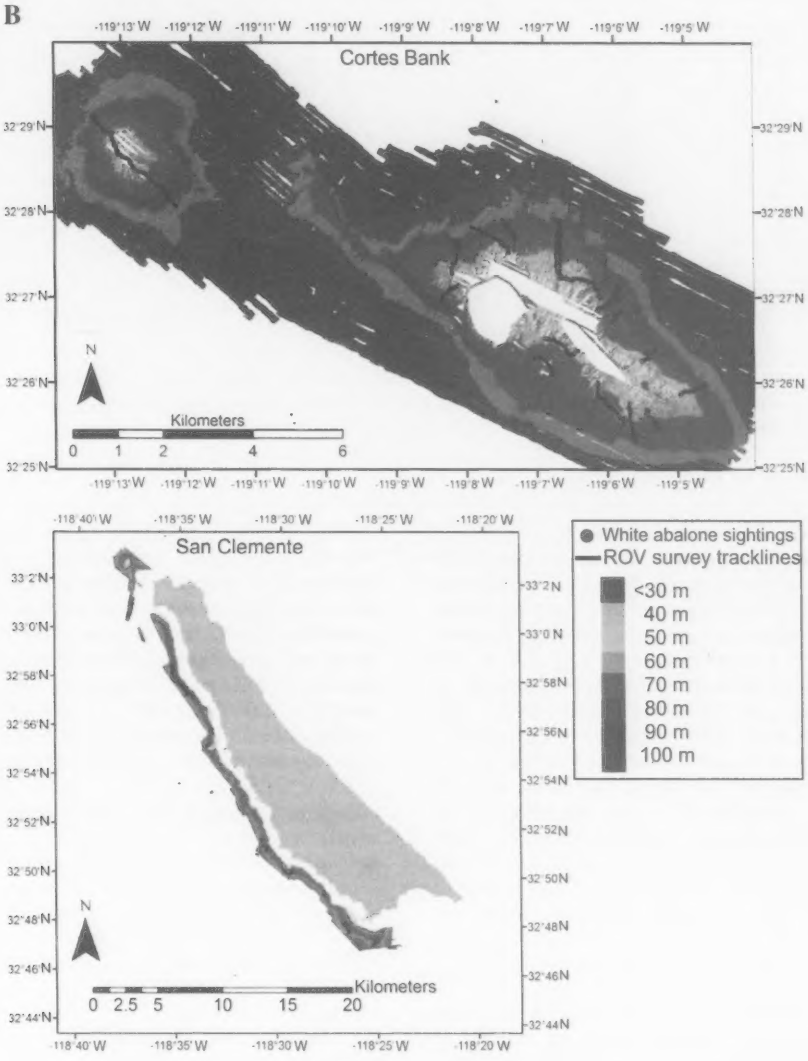

Figure 1 (continued)

algal cover in segments containing abalone, and those where abalone were absent for the Tanner Bank 2002 survey. For the purposes of PCA, transects were divided into 100-m segments. All PCA coefficients were plotted initially to examine relationships between abalone presence and absence and defined variables. Coefficients from the most influential variables were then plotted to examine these relationships more closely.

Transects varied in length from 0.4 to 6 km, although most transects were close to 1 km in length. To estimate abalone densities we attempted to search within a particular 10 m depth interval during each transect. When this was not possible, transects were poststratified by depth interval (10 m), because results of preliminary surveys provided evidence of the prevalence of white abalone within particular depth ranges. For the few cases (2) where poststratification yielded a search area of less than 100 m^2, the data for these areas were excluded from the analysis because densities would be artificially inflated. We calculated density per unit of area for each transect and stratified transects by three depth intervals (30–40 m, 40–50 m, and 50–60 m) to test for differences among depths and sites using Kruskal-Wallis nonparametric techniques on ranked data (Systat vers. 11, Systat Software Inc., Point Richmond, CA). The mean depth of abalone occurrence was tested

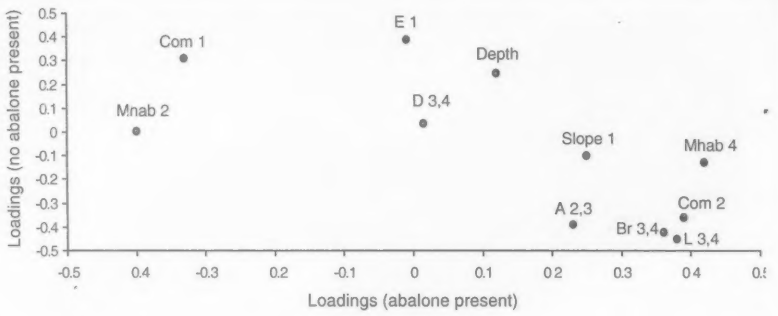

Figure 2

Summary results of principal component analysis for the 2002 Tanner Bank survey with white abalone (*Haliotis sorenseni*) present (*x*-axis) and no white abalone present (*y*-axis). See Table 1 for abbreviations and habitat descriptions.

for differences among sites with a one-way ANOVA. Depth and size distributions were compared among sites with a Kolmogorov-Smirnov (K-S) test. To estimate population sizes at each site, densities were applied to depth-area polygons derived from multibeam sonar bathymetry.

To examine the fine-scale spatial distribution of white abalone on the banks we determined and plotted linear distances between individuals along transects and recorded the number of groups (individuals within 2 m of another abalone) versus individuals (no other abalone within 2 m). Additionally, the distances between all individuals at each site were calculated, and for each abalone the distance to the nearest subsequent abalone sighting was determined. This was not a traditional nearest neighbor analysis, because transects were not designed for such an analysis. To test the degree of dispersion of the population on a broader scale, the cumulative number of white abalone observed within 250-m^2 segments of transect between 40 and 50 m depth (the depth range with the highest abalone densities) at Tanner Bank in 2002 were fitted to a negative binomial distribution (Elliott, 1977). The Tanner Bank 2002 surveys were appropriate for this analysis because of the high number of abalone sightings there.

Results

Habitat

The amount of rocky habitat between 30 and 60 m depth at Tanner Bank, Cortes Bank, and the west side of San Clemente Island was 1359, 1139 and 889 ha, respectively (Fig. 1). Side-scan sonar data indicated that the majority of the sea floor shallower than 60 m at all sites is hard substrate (Fig. 1). High-resolution bathymetry from multibeam sonar revealed a complex structure on the offshore banks. Tanner Bank and Cortez Bank are uplifted anticlines that have been eroded by wave action from the northwest during past periods of lower sea level (Vedder et al., 1986). Erosion of more recent geologic units has exposed erosion-resistant marine sedimentary and volcanic rocks that through differential erosion have developed layering and fracture features favorable to abalone. San Clemente Island is on the uplifted southern side of the San Clemente fault (Vedder et al., 1986), and is composed of erosion-resistant volcanic rocks of the same age as those at Tanner and Cortez Banks.

Microhabitat analysis

At Tanner Bank in 2002, white abalone were generally found in association with two species of brown algae (*Laminaria farlowii* and *Agarum fimbriatum* [88% of white abalone sightings included one or both species]), a foliose red alga (*Rhodymenia* spp. [45% of sightings]), genticulate coralline algae (*Calliarthron* spp.) and *Corallina* spp. [79% of sightings]), and encrusting coralline algae (*Lithothamnion* spp. [100% of sightings]). The brown alga *Dictyotaceae* spp. was present in 9% of white abalone sightings (mostly in deeper waters), and *Eisenia arborea* in 6% of sightings (mostly in shallower waters).

A PCA examination of these data revealed a strong positive relationship between the presence of white abalone and several factors; the strongest loadings occurred with depth, microhabitat type (Mhab 4 (deformed with sand)), the magnitude of seafloor slope (slope 1, flat), moderate seafloor complexity (Com 2 (low)), and the relative abundance (common or abundant) of brown algae A (*Agarum fimbriatum*), L (*Laminaria* spp.), and Br (brown algae spp. in general); (Fig. 2, Table 1). In contrast, a strong negative relationship existed between zero white abalone density and habitat characteristics; the strongest negative relationships occurred with the frequent presence of various algal species (same as above). There were strong positive relationships

between zero white abalone density and the presence of *Eisenia arborea*, and zero white abalone density and low seafloor complexity (com 1 [very low]).

Although detailed habitat analyses were not completed for the 2003 Cortes Bank survey, we noted the presence of the brown algae *Pterygophora californica* and *Cystoseira* spp. (both absent at Tanner Bank in 2002), and the apparent absence of *Dictyotaceae* spp. in deeper waters.

Abalone abundance, depth, and size distribution

A total of 258 individual white abalone were identified in all surveys, and the highest numbers were seen at Tanner Bank in 2002 (19.8 abalone/ha, Fig. 3, Table 2). Densities ranged from 0.0 abalone/ha (San Clemente Island, 50–60 m depth range) to 19.8 abalone/ha (Tanner Bank 2002, 40–50 m depth range, Fig. 3, Table 2). Very few individuals of other haliotids (5 pink and 3 red) were identified. Search effort was focused on the 30–60 m depth range after preliminary results at Tanner Bank indicated that white abalone inhabit this depth range, but surveys were conducted at shallower and deeper depths at each site to confirm these findings. No abalone were found shallower than 32 m or deeper than 61 m at any site, and therefore the results of these surveys were not included in the analysis. Overall densities differed significantly between surveys (n=162, Kruskal-Wallis test, test statistic=23.76, P<0.0001). Densities within surveys grouped by 10 m depth bins only differed significantly by depth for the Tanner Bank 2002 survey (n= 33, Kruskal-Wallis test, test statistic=10.45, P<0.01, Fig. 3). The total number of abalone shells ranged from 44 (San Clemente Island) to154 (Cortes Bank). The depth distribution of white abalone for all surveys combined reveals that white abalone were stratified by depth overall, although search effort was focused on the middle depth ranges (Figs. 3 and 4). The depth distribution of empty shells was similar to that of live white abalone (31–61 m), although there were several (<10) shells found

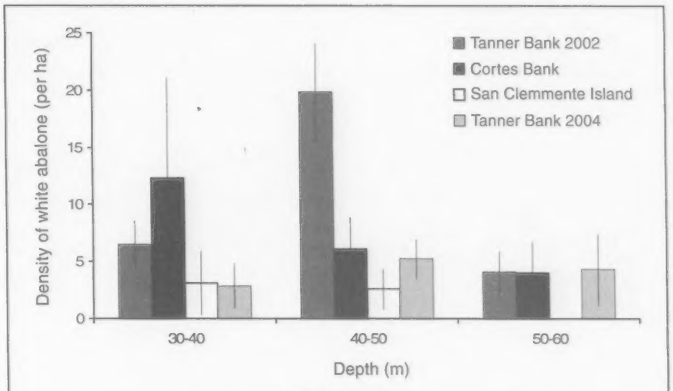

Figure 3

Density of white abalone (*Haliotis sorenseni*) by depth at Tanner Bank (two years), Cortes Bank, and San Clemente Island. Error bars represent standard error.

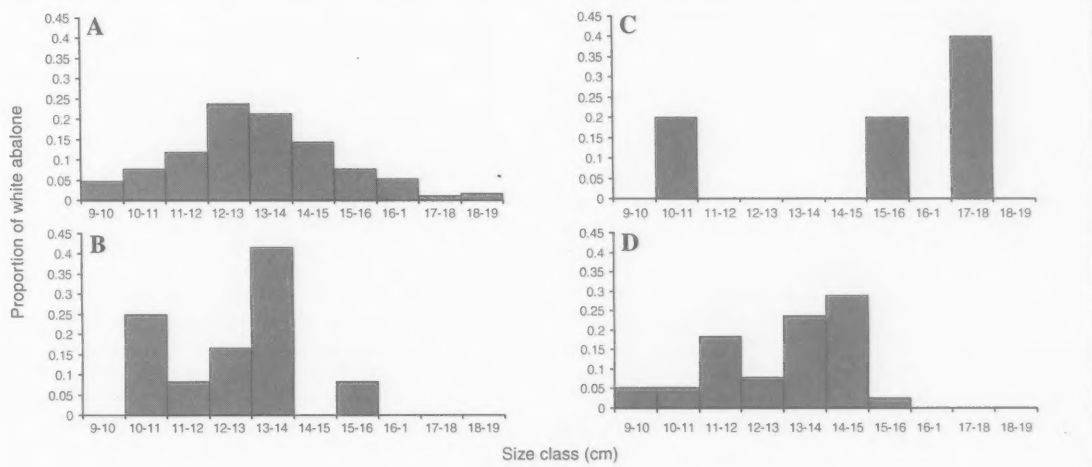

Figure 4

Size distribution for white abalone (*Haliotis sorenseni*) at (**A**) Tanner Bank, 2002 (n=168), (**B**) Cortes Bank (n=12), (**C**) San Clemente Island (n=5), and (**D**) Tanner Bank, 2004 (n=35).

Table 2

Density of white abalone (*Haliotis sorenseni*), area surveyed by the ROV, habitat area and population estimates by depth strata for Tanner Bank, Cortes Bank, and San Clemente Island.

	Tanner Bank			
Depth (m)	Density (/ha ±SE)	Area surveyed (ha)	Habitat area (ha)	Population
30–40	2002: 6.5 ±2.1 2004: 2.9 ±1.9	2002: 3.5 2004: 0.93	245	2002: 1592.5 ±514.5 2004: 710.5 ±465.5
40–50	2002: 19.8 ± 4.3 2004: 5.2 ± 1.7	2002: 5.0 2004: 3.9	425	2002: 8415.0 ±1827.5 2004: 2210.0 ±722.5
50–60	2002: 4.08 ±1.8 2004: 4.3 ±3.1	2002: 2.3 2004: 1.7	689	2002: 2811.1 ±1240.2 2004: 2962:7 ±2135.9
Total	2002: 13.0 ±3.5 2004: 6.1 ±1.5	2002: 10.8 2004: 6.5	1619	2002: 12,818.6 ±3582.2 2004: 5883.2 ±3323.9

at relatively shallow (<25 m) and one shell found at a relatively deep depth (72 m).

The sizes of white abalone at all sites ranged from 9.0 to 19.0 cm (Fig. 4). No small abalone were observed, although turban snails smaller than 6 cm were detected by using ROV sampling methods. Size distributions differed significantly for comparisons made between Tanner Bank 2002 and Cortes Bank, and Tanner Bank 2002 and San Clemente Island (K-S test, $P<0.01$, Fig. 4). There was an apparent shift in size distributions between years at Tanner Bank; fewer large animals were found in 2004 than in 2002, although the overall size distributions did not differ significantly between years (K-S test, $P=0.19$, Fig. 4). The size distribution at Cortes Bank included animals in the mid size range, and no abalone in the smallest or largest size ranges. Densities at San Clemente Island were too low to show any real pattern in size distribution (Fig. 4). The mean size of abalone ranged from 12.4 cm to 13.7 cm and did not differ significantly between surveys (ANOVA, $P>0.05$).

Site-specific white abalone population estimates were based on the amount of available habitat quantified from the results of multibeam sonar surveys and white abalone density estimates determined from data from ROV surveys. The total population of white abalone on Tanner Bank based on 2002 density measurements was estimated at 12,819 ±3582 (SE), whereas the total population estimate based on 2004 density measurements was 5883 ±3324. The total population on Cortes Bank was estimated at 7366 ±5340 (SE), and that at San Clemente Island was estimated at 1938 ±1598 (SE; Table 2).

White abalone reproductive potential

Eighty-nine percent of white abalone at all sites were observed as singletons, and only 6% were observed in groups. Group sizes ranged from two to five individuals and the largest group was observed at Tanner Bank in 2002. There were no sightings of abalone in groups at Tanner Bank in 2004. White abalone were not found frequently in groups during any of the surveys, and the observed number of individuals within 250-m^2 subsamples within the 40–50 m depth range at Tanner Bank in 2002 did not differ from values predicted by the negative binomial distribution (chi-square=4.9, $P=0.67$).

The results of an analysis of distances between sightings indicated that less than 25% of individual abalone were located within 5 m of one another for all surveys. The majority of individuals (60%) were over 20 m away from another sighted abalone. The survey with the highest proportion of abalone located within a distance of 20 m of another individual was that at Tanner Bank in 2002. In regard to potential mating pairs, out of a possible 19,503 combinations of mating pairs, only 202 were within 30 m from one another at Tanner Bank in 2002, 4 out of 231 pairs at Cortes Bank, 3 out of 12 pairs at San Clemente Island, and 10 out of 861 pairs at Tanner Bank in 2004.

Discussion

Few areas in U.S. waters have been adequately mapped to reveal detailed bathymetry or substrate characteristics. Consequently, our knowledge of the amount of habitat available for benthic marine organisms is so inadequate that one can only speculate about overall population sizes. White abalone populations in southern California are no exception; all previous estimates of the amount of suitable habitat available for white abalone have been based on the assumption made by Thompson et al. (1993) that 3% of the sea floor between 25 m and 65 m was rocky substrate (Davis et al., 1998;

Cortes Bank				San Clemente Island			
Density (/ha ±SE)	Area surveyed (ha)	Habitat area (ha)	Population	Density (/ha ±SE)	Area surveyed (ha)	Habitat area (ha)	Population
12.3 ±8.8	2.6	232	2853.6 ±2041.6	3.1 ±2.8	0.8	392	1215.2 ±1097.6
6.1 ±2.8	1.5	423	2580.3 ± 1184.4	2.6 ±1.8	2.4	278	722.8 ±500.4
4.0 ±2.7	0.7	483	1932 ±2114.1	0	0.7	219	0
8.0 ±3.1	4.8	1138	7365.9 ±5340.1	1.5 ±0.2	3.9	889	1938 ±1598

Hobday and Tegner, 2000; Hobday et al., 2001). Using this assumption, the total amount of white abalone habitat in southern California was estimated to be only 752 ha (Davis et al., 1998; Hobday et al., 2001). The results of surveys from the present study at only three sites (Tanner and Cortes Banks and San Clemente Island) revealed 3646 ha of rocky substrate between 30 and 60 m, which is much higher than estimates based on the 3% rocky habitat assumption. Thus, the total available habitat area for white abalone and other benthic dwelling organisms in southern California is likely far greater than previously reported.

The definition of available white abalone habitat, however, may need further refinement if white abalone exhibit a preference for a certain type of rocky substrate. Cochrane et al. (2005) suggested that white abalone prefer the edges of reefs at the sand-rock interface rather than the areas in the middle of the reef. Although there is some qualitative evidence supporting this idea, there have been no conclusive studies on specific habitat preferences. The only conclusion that can be drawn in relation to habitat preference from the present study is that white abalone are not typically found in areas with no rock (i.e., sand only). Even if white abalone were found only at the sand-rock interface, our estimates of available habitat would still far exceed past estimates. Although the time and effort involved in mapping habitat may lead to the temptation to make broad generalizations to estimate habitat types and amounts, the results of this study have shown that specific habitat mapping is necessary to accurately identify the amounts of each type of habitat existing in a particular area.

The depth distribution of white abalone at these three sites was grouped into three depth bins (30–40 m, 40–50 m, and 50–60 m) and was less stratified than predicted according to preliminary surveys at Tanner Bank. The number of abalone was highest in the middle depth bin (40–50 m) at Tanner Bank during 2002 and 2004, but only significantly so in 2002. The highest number of abalone observed at Cortes Bank was in the shallowest depth bin (30–40 m). Too few abalone were sighted at San Clemente Island and they were not included in the analysis. These results indicate that there are not clear, broad trends in depth distribution that can be applied to all sites, although the deepest depth bin did yield the fewest abalone sightings at all sites. It is also possible that the only realistic trends observed were those at Tanner Bank in 2002 because of the relatively large number of animals observed at this site.

The white abalone population in California has been estimated to number less than 3000 (Davis et al., 1998; Hobday and Tegner, 2000; Hobday et al., 2001). In this study a total of between 15,187 and 22,123 white abalone was estimated at two offshore banks and one island location. Our population estimate is greater for two reasons: 1) the multibeam sonar maps revealed more habitat than was previously known to exist, and 2) search effort, and therefore the calculation of density, was dependent on suitable habitat, i.e., densities were not artificially deflated by including portions of surveys conducted in inappropriate habitat (e.g., sand).

The highest densities (19.8 abalone/ha between 40 and 50 m) were observed at Tanner Bank in 2002. Previous surveys at Tanner Bank underestimated habitat area and included the entire search area without regard to depth or habitat to determine density. A re-examination of data from surveys conducted by the Delta submersible in 1999 at Tanner Bank (Haaker et al.[2]) yielded an overall density of 15.7 abalone/ha. This value varies only slightly from our overall density esti-

mate of 13.0 abalone/ha. Densities were lower overall in our surveys conducted at Tanner Bank in 2004, and the most significant differences were apparent in the 40–50 m depth range. These lower densities in surveys conducted only two years after initial surveys are noteworthy and worrisome, especially because Tanner Bank is a site where the population was thought to be relatively stable.

The density of white abalone prior to commercial and recreational exploitation is poorly known, and the few reported estimates are the subject of considerable speculation. Tutschulte (1976) reported an estimate of white abalone density of 2300 abalone/ha, based on three 10-m^2 quadrats. Because of the small sample size and lack of replicate sites, caution should be used when applying this estimate to all of California. However, it is important to note that one cluster of five white abalone was observed in the present study, which would lead to a local density close to that reported by Tutschulte (1976). It is also of interest to note that Shepherd et al. (2001) suggested that once populations of *Haliotis laevigata* reached densities below 0.25 abalone/m^2 (2500 abalone/ha) management action should be taken, and therefore estimates of 0.23 abalone/m^2 reported by Tutschulte (1976) were not extremely high.

More recently Rogers-Bennett et al. (2002) used historical landings data and the habitat area estimated by Davis et al. (1998) and Hobday et al. (2001) in an attempt to reconstruct past population densities. Applying the 3% rocky habitat criteria referred to above (Discussion section, paragraph 1) (Thompson et al., 1993), Rogers-Bennett et al. (2002) calculated a density of 479 abalone/ha for all of California and a density of 1623 abalone/ha for San Clemente Island, where 75% of the landings were reported. These densities are lower than those reported by Tutschulte (2300 abalone/ha; 1976), but the more recent estimate is also too high because the proportion of rocky habitat is greater than 3%, as observed in the present study. The maximum density observed in the present study (19.8 abalone/ha) is only an order of magnitude less than Rogers-Bennett et al.'s (2002) calculation of historic density for all of California (479 abalone/ha), but is two orders of magnitude less than the estimates by Tutschulte (2300 abalone/ha, 1976). Regardless of the problem of inflated density estimates, the densities observed in the present study at San Clemente Island were less than 5 abalone/ha at all depths, which is astoundingly lower than the 1623 abalone/ha calculated by Rogers-Bennett et al. (2002).

Whether the existing white abalone populations are viewed as viable depends largely on the validity of estimates of past population distributions and densities and on establishing confidence in current density estimates. Total abundance of individuals becomes irrelevant if these animals are distributed such that densities within a particular area are below the critical level necessary for successful reproduction. The relatively deep range of *H. sorenseni* is outside the range of dense macroalgal growth, and therefore we can assume that the ROV does an adequate job in identifying animals within its field of view (2 m). Based on the assumption that we are actually sighting nearly all of the animals that are within the search range, our data indicate that the majority of individuals at these sites are greater than 5 m (linear distance) from any other individuals along and between transects, and that many are over 30 m away from a potential mate. These distances well exceed what has been shown to be a critical minimum distance (≤2 m) for successful spawning and fertilization in other species of abalone (e.g., *Haliotis laevigata*; Shepherd and Brown, 1993; Babcock and Keesing, 1999; Shepherd et al., 2001). The large distances between individuals coupled with density estimates that are several orders of magnitude lower than those necessary for a viable population (Shepherd et al., 2001) would indicate that white abalone populations are currently in a dire state.

Despite generally large distances between individuals, an analysis of dispersion within the population surveyed at Tanner Bank in 2002 showed a large proportion of individual sightings within 30 m of another sighting. Additionally, there was a high degree of contagion between individuals in 250-m^2 subsamples at depths of 40–50 m. It may be true that white abalone at this site are aggregated on a larger scale, indicating that certain habitats within their most prevalent depth range (40–50 m) may promote higher survival of white abalone. However, ultimately, if animals are not packed densely enough at smaller scales, successful spawning and fertilization will not occur. This study highlights the importance of establishing accurate density estimates at appropriate scales for guiding assessments of population viability and future enhancement protocols.

The mean sizes of white abalone observed in the present study varied little between sites and were comparable to those observed during 1999 submersible surveys at Tanner Bank and Cortes Bank (Behrens and Lafferty, 2005). The size distribution of white abalone did differ slightly between the two banks and island location. More notable was an apparent shift in the size distributions of animals observed at Tanner Bank in 2002 versus those observed in 2004. Unlike in 2002, there were no large individuals observed in 2004, indicating a possible die-off of older individuals and a lack of new, younger individuals to fill this size class. No white abalone smaller than 9.0 cm (approximately three years old; Tutschulte, 1976) were observed at any of the sites. If this were a self-sustaining population, smaller individuals indicating recruitment from several preceding year classes would be present, although the likelihood of sighting abalone recruits and juveniles younger than three years is not very high. Juvenile white abalone shells are mottled red in color and settlement occurs on pink crustose coraline algae-covered rocks, thus making them very cryptic during the first few years of life. Even during historic periods when white abalone density was much higher than cur-

rent levels, juveniles were observed on extremely rare occasions (Owen[4]). Thus, the absence of small individuals during ROV observations does not rule out recent recruitment to this population. Consequently, although recruitment in the last three years may be undetectable, recruitment from the last three decades should be evident in our surveys.

Conclusions

The use of detailed sonar mapping techniques has proven to be an invaluable method to estimate amounts of different habitat types for the purposes of quantifying marine organisms within their specific habitat. Specifically, white abalone restoration efforts would be greatly enhanced by more surveys incorporating high-resolution bathymetric maps that would serve to better define the characteristics of suitable white abalone habitat. Our concept of what a viable white abalone population is would benefit from more accurate density estimates for other areas within the historic range and from a better understanding of how white abalone are distributed within populations.

The ultimate goals of recovery and eventual removal of white abalone from the Endangered Species List depends upon establishing confidence in the demographic parameters that define a viable white abalone population. It has become apparent that conducting studies such as this one, with continuing efforts to improve sample standardization techniques over time, is critical to achieving recovery goals.

Acknowledgments

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Experiments in gear configuration to reduce bycatch in an estuarine squid-trawl fishery

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Abstract—Three experiments were performed in an estuarine squid-trawl fishery in New South Wales, Australia, to test modifications to trawl nets. Lateral mesh openings were experimentally increased and physical bycatch reduction devices (BRDs) were placed in codends. These modifications aimed to reduce nontargeted catches of fish, while maintaining catches of the targeted broad squid (*Photololigo etheridgei*) and bottle squid (*Loliolus noctiluca*). Compared to conventional codends made with 41-mm diamond mesh, codends made with different posterior circumferences and larger 45-mm mesh had no significant effect on the catches of any species. The best performing configurations involved the installation of BRDs designed to separate organisms according to differences in behavior. In particular, versions of a composite square-mesh panel reduced the total weight of bycatch by up to 71% and there was no significant effect on the catches of squid. The results are discussed in terms of the probable differences in behavior between fish and squid in codends. After this study, a square-mesh panel BRD was voluntarily adopted throughout the fishery.

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The incidental catch of nontarget organisms (termed "bycatch") by commercial fishing gears will remain an important issue in the management of fisheries. Article 7.6.9 of the Food and Agriculture Organization's Code of Conduct for Responsible Fisheries (FAO, 1995) notes "States should take appropriate measures to minimize waste, discards, catch by lost or abandoned gear, catch of non-target species, both fish and non-fish species, and negative impacts on associated or dependent species, in particular endangered species." Several options are available for achieving these aims (Hall, 1996), but the most common strategy involves technological improvements to fishing gears that reduce unwanted mortality due to fishing (Kennelly and Broadhurst, 2002).

Much research into gear design to reduce bycatch has been undertaken in demersal trawl fisheries and especially those targeting shrimp (for reviews see Kennelly, 1995; Broadhurst, 2000). This research reflects the seriousness of bycatch issues in these fisheries and, in particular, the incidental mortality of key species such as marine turtles and juveniles of commercially and recreationally important fish. Considerably less work has been done on bycatch in other fisheries, including those targeting cephalopods.

The global catch of squid has been estimated at 2.8 million tonnes (t) per year (FAO[1]). Squid are harvested with highly-selective jigs or less selective gill nets, seines and, more commonly, trawls (Rathjen, 1991; Morais da Cunha and Moreno, 1994; Simón et al., 1996). Large-scale use of pelagic gill or drift nets has been restricted because of concern about incidental catches (e.g., Burke et al., 1994; Piatt and Gould, 1994). Despite their widespread use, very little work has been done to modify towed gears so that they selectively harvest squid. In one of the few studies relevant to this issue, Glass et al. (1999) attached video cameras to the anterior sections of trawls targeting longfin squid (*Loligo pealeii*) in the Atlantic Ocean and observed that squid positioned themselves considerably higher in the trawl than fish. It was suggested that this difference in behavior could be used to separate catches.

[1] Food and Agriculture Organization (FAO). 2005. FAO Fisheries Global Information System. www.fao.org/fi/figis [accessed on 23 Nov 2005]. Average annual global production of all squid species for 2000 to 2003.

In New South Wales (NSW) Australia, arrow squid (*Nototodarus gouldi*), mitre squid (*Photololigo* sp.) and southern calamari (*Sepioteuthis australis*) are important in the legally retained bycatch from fish and prawn trawlers working in oceanic waters. In addition, two species of squid are specifically targeted by up to 20 trawlers with modified, single-rigged prawn trawls in Broken Bay (Fig. 1). Broad squid (*P. etheridgei*) (typically 30–290 mm mantle length [ML] when harvested) represent the majority of the total catch (approximately 25–50 t per year since 1997), although the smaller bottle squid (*Loliolus noctiluca*) (30–90 mm ML when harvested) are also retained and sold, primarily as bait for recreational anglers. Additional details on the local biology of *P. etheridgei* can be found in O'Donnell (2004).

The designs of trawls used to catch these squid vary among operators, but all are restricted by lengths of the headline (<11 m) and sweeps (<5 m) and minimal and maximal mesh openings of 40–60 mm in the body and 40–45 mm in the codend. To maximize catches of the smaller bottle squid, all operators use codends of the minimal legal mesh size of 40 mm, with anterior sections of 100 meshes in circumference attached to posterior sections of at least 150 meshes in circumference (made with thick twine), which are designed to reduce lateral-mesh openings (Broadhurst and Kennelly, 1996).

The configuration of conventional codends in the Broken Bay squid-trawl fishery means that these trawls are poorly selective and therefore, in addition to the targeted squid, they also retain large quantities of bycatch. Preliminary data from a 3-year observer-based study of catches in the early 1990s (DPI[2]) indicated a bycatch-to-squid ratio of up to 4:1 (by weight). Although a subset of this bycatch includes some species that the fishermen are legally permitted to retain, most of the bycatch is small, unwanted fish, including juveniles of several commercially and recreationally important species. Concerns over the mortality of these individuals and the negative impacts on stocks led us to test the utility of modifications to fish- and prawn-trawl codends for improving selection of species in squid trawls. Such experimental work has not previously been completed in squid-trawling fisheries.

A series of explicit hypotheses were tested in the fishery. It was proposed that devices designed to reduce bycatch would 1) cause differential changes in catches, by reducing bycatch but causing no important reduction in catches of squid; 2A) not cause disproportionate bycatch of small or large fish (i.e., would not influence the distributions of sizes of fish caught); 2B) not cause differential effects, so that subsequent incidental catches had similar mixtures of types and relative abundances of fish species as before; and, 2C) not cause relatively larger catches of particular fish species, nor of juveniles of commercial species.

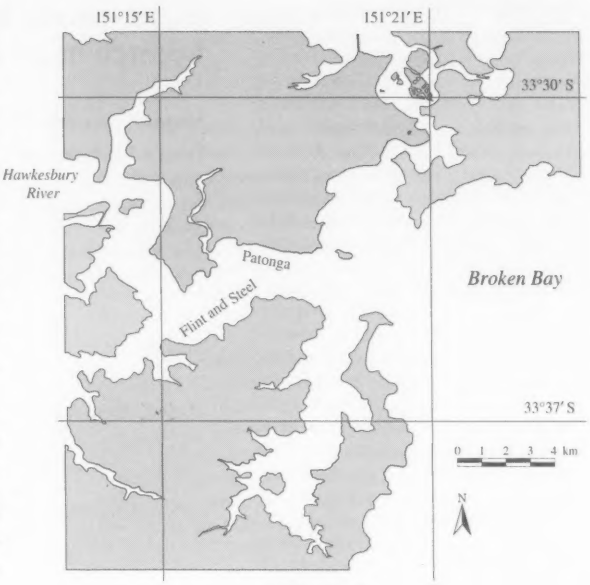

Figure 1

Location of Broken Bay and the two areas trawled (Patonga, and Flint and Steel). Broken Bay is 35 km north of Sydney, New South Wales, Australia.

Materials and methods

This research was completed on two commercial squid-trawl grounds in Broken Bay NSW (Fig. 1) between February and September 2002 by using a chartered squid trawler (9.2 m in length). The vessel was rigged with a single, conventional 4-seam otter trawl made from 60-mm (all mesh sizes refer to stretched opening) polyethylene (PE) netting (headline of 11 m; Fig. 2) towed between 0:8 and 1.8 m/s over a sandy substratum at depths ranging from 5 to 15 m. A zipper (Buraschi S146R, Milan, Italy, 1.5 m in length) was attached at the posterior body of the trawl to facilitate changing codends (Fig. 2).

Codends and BRDs examined

Five codends of different design were made from dark PE netting with total lengths and anterior fishing circumferences (i.e., the expected circumference of the codend during towing—[Broadhurst et al., 1999]) of 2.4 and 1.5 m, respectively (Fig. 3, A–E). All codends had zippers (Buraschi S146R, 1.5 m in length) attached at their anterior ends. Four of the codends were made within existing regulations and had anterior sections made from 40-mm knotted netting (2-mm diameter-ø twisted twine) with a length and circumference of 35

[2] DPI (New South Wales Department of Primary Industries). Unpubl. data. 1992. [Data are on file at New South Wales Department of Primary Industries, PO Box 21, Cronulla, 2230, NSW, Australia.]

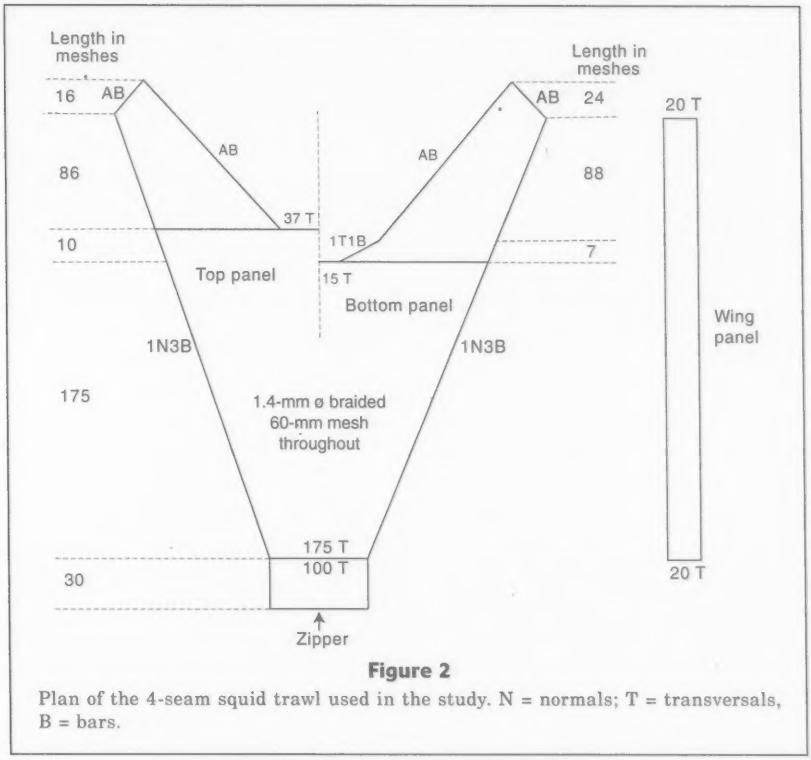

Figure 2

Plan of the 4-seam squid trawl used in the study. N = normals; T = transversals, B = bars.

and 100 meshes, respectively, and posterior sections with a length of approximately 1 m, but different mesh circumferences and sizes (all meshes were made from 3-mm ø braided twine; Fig. 3, A–D). The first codend (41/150) represented commercially used designs with a posterior section of 41-mm mesh and a circumference of 150 meshes (Fig. 3A). The second codend (41/100) had a posterior section made from the same mesh, with a circumference of 100 meshes (Fig. 3B). The third and fourth designs (45/150 and 45/100, respectively) had posterior sections with the same circumferences as those above, but were made from 45-mm mesh (Fig. 3, C and D). The fifth codend design (termed the "square-mesh codend") was made entirely of 30-mm mesh (1.4-mm ø twisted twine) hung from the bar (i.e., the meshes were oriented so that they were square shaped) and had a total length and fishing circumference of 144 and 90 bars, respectively (Fig. 3E).

Four variations of behavioral-type bycatch reduction devices (BRDs) were tested in combination with certain codends (Fig. 3, F–I). All BRDs were installed in the top anterior section of the relevant codend at a distance starting 1.1 m anterior to the last row of meshes in the posterior section according to the specifications provided by Broadhurst et al. (2002). The first BRD (the diamond BRD; see Broadhurst et al. [2004]) was a diamond-shaped opening (11×11 bars) cut into a conventional 41/150 codend (Fig. 3F). The second and third BRDs were composite square-mesh panels (CSMP; Broadhurst and Kennelly[1996]) with 90- or 75-mm mesh, respectively, hung from the bar in the main escape panels and were inserted into the conventional 41/150 and 41/100 codends. These modified codends were called the "90-CSMP" and "75-CSMP" codends (Fig. 3, G and H). The fourth BRD was inserted into the square-mesh codend (termed the "75-panel codend"; Fig. 3I); it was a simple panel of 75-mm mesh hung from the bar (and having the same dimensions as that used in the CSMP codend).

Experimental procedure

Three independent experiments were completed during 2002 to identify an appropriate combination of codend and BRD that minimised bycatch whilst maintaining catches of squid. Experiment 1 (25 February–1 March 2002, five days, two replicate hauls/day) tested predictions about the effect of 1) changing the posterior codend circumference within the maximal and minimal codend mesh sizes legally permitted in the fishery; and 2) using the diamond and CSMP BRDs located in the commercially used 41/150 codend. Experiment 2 (29 July–9 August 2002, 10 days, two replicate hauls/day) repeated experiment 1 above (but with additional replication to increase the power to differentiate between the codends) and also tested the effectiveness of the square-

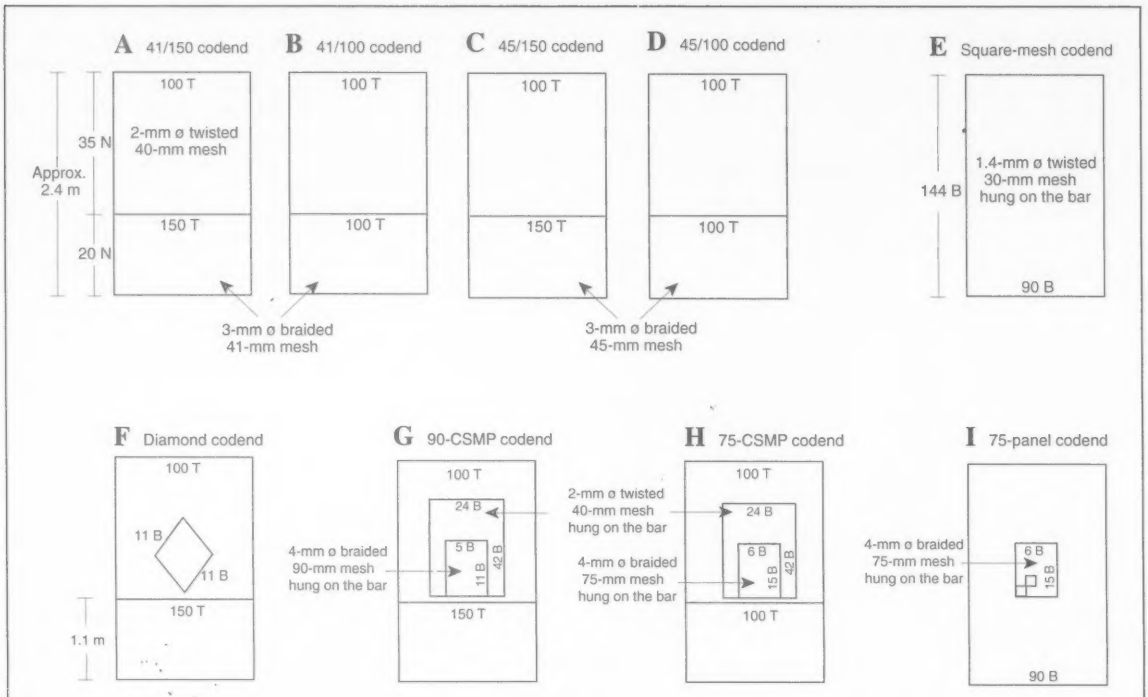

Figure 3

Schematic representation of the codends and bycatch reduction devices tested during the experiments. The 41/150 codend is the conventional design used in the fishery. N = normals; T = transversals, B = bars.

mesh codend. Experiment 3 (26 August–6 September 2002, 10 days, three replicate hauls/day) compared the 41/100 and square-mesh codends (the most appropriate non-BRD codends; see Results section), with and without their respective 75-CSMP and 75-panel BRDs installed.

In each experiment, the daily position and order of the codends being tested were determined randomly and they were alternately used in normal commercial hauls of 30-min duration between 0700 and 1500 hours. Depending on the number of codends being tested, we attempted two or three balanced replicates of each treatment on each day. Haul location was determined by the skipper and varied between the two squid trawl grounds in Broken Bay (Fig. 1) according to the presence of jellyfish, *Catostylus* sp., which reduced the efficiency of the trawl. Data collected from each replicate haul included the numbers and weights of all taxa and the sizes of commercially and recreationally important species. When large numbers (several hundred) of any species were caught, a randomly selected subsample (approximately 25–50% of the total) was measured. Fish were measured to the nearest 0.5 cm fork length; carapace lengths of crustaceans were measured to the nearest 0.1 cm.

Results

Bycatch and target squid

The primary hypothesis for this study was that the devices designed to reduce bycatch would cause changes in catches, by reducing bycatch but causing no important reduction in the catches of squid. This hypothesis was tested by using univariate statistical methods applied to the results from all three experiments. In Experiment 1, the diamond and 90-CSMP codends caught less bycatch (about 74% less on average) than the other types of gear (Table 1). About 50% of the bycatch were discards, including teleost fish such as tailor (*Pomatonus saltatrix*) and mulloway (*Argyrosomus japonicus*). There were, however, no significant reductions in catches of squid, although catches were smaller with the diamond codend. As a result, later experiments were mostly done with larger mesh sizes. There were no effects of altering other components of the gear (circumference or mesh-size of the codend). Catches of squid were significantly different on the two days (Table 1A), but there was no interaction with the type of codend; therefore differences among types of gear were consistent. Sources of variation that were determined to be nonsignificant at $P>0.25$

Table 1

Analyses of catches using six types of gear from experiment 1 during February–March 2002. Data are weights of catches from Flint and Steel, fished for 2 different days (a random factor). Codend (a fixed factor) is the comparison of 41/150, 41/100, 45/150, 45/100, diamond and 90-CSMP (composite square-mesh panel) codends. $n \doteq 2$ replicate hauls for each treatment on each day.

A Analyses of variance

			Bycatch			Squid		
Source of variation		df	Mean square	*F*	*P*	Mean square	*F*	*P*
Codend	$= C$	5	1.51	3.16[a]	<0.04	0.24	0.63[a]	>0.65
Day = *D*	$= D$	1	0.46	0.96[a]	>0.30	2.50	6.51[a]	<0.05
$C \times D$		5	0.39[p]			0.33[p]		
Residual		12	0.51[p]			0.40[p]		
[p]Pooled residual		17	0.48			0.38		

B Mean untransformed weight (kg, [±standard error, n=4]) of bycatch and squid per haul and Student-Newman-Keuls tests; "<" indicates significant differences at $P<0.05$; "=" indicates $P>0.05$.

	Codend											
	Diamond		90-CSMP		41/100		41/150		45/100		45/150	
Bycatch	7.7 (2.3)	=	6.4 (1.7)	<	23.1 (6.1)	=	22.3 (2.2)	=	24.8 (6.9)	=	17.3 (7.0)	
Squid	2.2 (0.6)	=	3.5 (0.8)	=	2.9 (0.7)	=	3.9 (1.2)	=	3.2 (1.2)	=	4.3 (1.2)	

were pooled and catches were transformed to natural logarithms to stabilize variances (Underwood, 1997).

A second analysis compared the diamond and 90-CSMP with the conventional 41/50 codend in two areas (in estuarine waters off Patonga, and Flint and Steel, see Fig. 1), to check consistency across fishing-grounds. A balanced set of replicated hauls with each type of gear was obtained. Again, the two BRDs caused large and significant reductions in bycatch compared with the conventional net. Although catches of squid were smaller, they were not significantly so and there was a large reduction in the ratio of weight of bycatch to weight of squid caught. Strikingly, although there was considerable variation from day to day and between locations in the amount of bycatch, there were no interactions with experimental gear used. Therefore, reductions in bycatch were consistent under the different conditions that are typical to the fishery.

Experiment 2 compared catches with the four codends without BRDs, as in experiment 1, with catches with the square-mesh codend. There were complex differences in the amount of bycatch caught with different types of gear, despite many catches being smaller than those in experiment 1. More bycatch was caught with the 45/150 codend than with the 41/150 codend (i.e., an effect of mesh size). This difference was, however, detected only for the 150 codend. There was also an effect of circumference of the codends (41/100 caught more bycatch than did 41/150), but only for the commercial (41-mm mesh) codend. This finding explains the significant interaction between mesh-size and circumference in the analysis in Table 2.

Again, although there were differences in amounts of bycatch, there were no significant or detected differences in catches of squid (Table 2, A and B); therefore it was possible to achieve reductions in bycatch without any notable effect on the commercial catch.

During experiment 3 catches were generally small and patchy. Data were very variable, but it was possible to complete five days of trawling with the 41/100 and square-mesh codends with or without their square-mesh BRDs. There was a very marked reduction in bycatch when a BRD was added to a codend, regardless of whether there was a square-mesh panel in the codend or not (Table 3A). Again, there were no influences on the catches of squid, but the ratio of weight of bycatch to weight of squid was smaller for both types of mesh when a BRD was added (analysis of ratios in Table 3B).

Sizes of species in bycatch

The secondary hypotheses of this study, that devices to reduce bycatch would 2A) not cause disproportionate bycatch of small or large fish; 2B) not cause differential effects; and, 2C) not cause relatively larger catches of particular species, were tested with multivariate statistical methods.

Analyses of sizes of bycatch were uniform in their outcome—there was no measurable difference on the size composition of species caught for any of the devices tested. As examples, two species of fish were present in

Table 2

Analyses of catches from experiment 2 during July–August 2002. Data are weights of catches from two locations (Patonga, Flint and Steel; a random factor), each sampled over four different days (randomly, nested in location). Square-mesh panels were compared with the 41/150, 41/100, 45/150, 45/100 codends. There were n = 2 replicate hauls of each gear on each day in each location.

A Analyses of variance

Source of variation		df	Bycatch			Squid		
			Mean square	F	P	Mean square	F	P
Treatment	$= T$	4	1.61			0.55		
Square-mesh vs. others	$= S$	1	0.55	0.87	>0.35	0.72	1.3	>0.20
Mesh: 41 vs. 45	$= M$	1	1.14	1.80	>0.15	0.47	0.8	>0.35
Circumference: 100 vs. 150	$= C$	1	2.40	3.80	<0.05	0.30	0.5	>0.45
$M \times C$		1	2.40	3.70	<0.05	0.57	0.71	>0.20
Location	$= L$	1	2.17			1.13		
$T \times L$		4	0.80[P]			0.19[P]		
Days (L)	$= D(L)$	6	4.9	7.10	<0.001	0.69	1.2	>0.25
$T \times D$		24	0.72[P]			0.62[P]		
Residual		40	0.56[P]			0.50[P]		
[P]Pooled residual		68	0.63			0.56		

B Mean weight (kg, (±standard error, n=16)) of bycatch and catch in various treatments

		Circumference (no. of meshes)			
		100	150	100	150
Mesh	41-mmm	56.8 (17.5)	28.1 (5.4)	14.6 (2.1)	11.6 (1.8)
	45-mm	44.6 (6.7)	60.0 (12.9)	13.2 (1.5)	13.9 (1.7)
	Square-mesh (30 mm)	48.7 (10.5)		15.2 (1.9)	

most hauls, were fairly abundant in bycatch, and were each represented by a range of sizes. Tailor (*Pomatomus saltatrix*) were grouped into five length classes with approximately equal numbers of fish in each class (140–145, 146–170, 171–195, 196–220, 221–280 mm); the snapper *Pagrus auratus* were also so grouped into five length classes (70–105, 106–120, 121–135, 136–155, 156–230 mm). Data were analyzed as the proportion of fish in each size class, to remove differences due to different numbers of fish caught in the various types of gear. Size classes were then used as variables in multivariate analyses to compare the various types of gear.

Using data from experiment 1, we detected no differences among types of gear in the proportional size frequencies of either tailor or snapper. The mean Bray-Curtis dissimilarities between pairs of samples were all very similar to the mean measures within samples (i.e., among replicates); therefore there was no suggestion of differences in size frequencies among types of gear for these species. Multidimensional scaling plots (not included, Clark and Gorley[3]) supported this result because the centroids of the size classes of both species were not clustered by type of gear.

Composition of bycatch

The types of species and relative abundances of species in the bycatch were analyzed from several times of sampling. Analyses used data without squid because numbers of squid are irrelevant to the bycatch. Typically, there were no detected differences in assemblages of species in the bycatch. One exception, in Experiment 2 is described. In our study, analyses of Bray-Curtis dissimilarities showed some differences among types of gear, where the square-mesh codend caught a different assemblage. It seemed that fewer whitebait (*Hyperlophus vittatus*) were being caught when the square mesh was used (this was confirmed by SIMPER[4] analysis, which showed that numbers of whitebait were an important variable for discriminating between samples). To test the validity of this conclusion, we performed analyses, omitting numbers of whitebait. This time, all differences

[3] Clarke, K. R., and R. N. Gorley. 2001. Primer version 5: user manual/tutorial, 91 p. Primer-E Ltd, Plymouth, U.K.

[4] See footnote 3.

Table 3

Analyses of catches from four codends (41/100, square-mesh, 75-panel, 75-CSMP [composite square-mesh panel]) from experiment 3 at Flint and Steel during August–September 2002. Data are weights of catches on five days, during each of which there were $n = 3$ independent hauls with each type of gear.

A Analysis of variance

			Bycatch			Squid			Ratio: bycatch/squid		
		df	Mean square	*F*	*P*	Mean square	*F*	*P*	Mean square	*F*	*P*
Mesh: 41 vs. square mesh	$= M$	1	0.9	1.4	>0.25	0.001	0	>0.95	0.3	0.8	>0.35
+BRD vs. –BRD	$= B$	1	4.5	6.6	<0.01	0.1	0.2	>0.60	2.4	3.1	>0.15
$M \times B$		1	2.5	3.6	>0.05	0.2	0.4	>0.50	1.0	0.4	
Days	$= D$	4	5.7	8.4	<0.001	0.7	0.7	>0.60	2.5	6.0	<0.001
$M \times D$		4	0.8[P]			0.5[P]			0.2[P]	0.4	>0.50
$B \times D$		4	0.8[P]			0.6[P]			0.8	1.8	>0.15
$M \times B \times D$		4	0.6[P]			0.4[P]			0.2[P]		
Residual		40	0.7[P]			0.6[P]			0.5[P]		
[P]Pooled residual		52	0.7			0.6			0.41	(48 df)	

B Multiple comparisons: mean weight (kg, (±standard error, n=30)) of bycatch, squid. and ratio of bycatch/squid; * indicates a difference (Student-Newman-Keuls test; P<0.05).

Bycatch		Squid		Ratio: bycatch/squid	
–BRD	+BRD	–BRD	+BRD	–BRD	+BRD
3.3 (0.5)	2.6 (0.4)*	1.6 (0.2)	1.6 (0.2)	6.0 (3.8)*	1.6 (0.4)

among types of gear disappeared. Whitebait are not an important concern for management in this fishery and results like these were not obtained in the other experiments; therefore no further consideration was given to this matter. Results from this study indicate that the composition of assemblages of bycatch was not altered by combinations of experimental gear and there were no detectable influences on particular species.

These multivariate results indicated that, with the exception of whitebait, none of the secondary hypotheses (2A, 2B, or 2C) could be rejected. These experiments did, however, have limited power to detected small effects because of the large variability of the catches and the relatively limited replication completed.

Discussion

The results demonstrated that the general concepts used to improve species selection in fish and shrimp trawls have similar application for squid. Nevertheless, the specific designs of modifications require careful consideration, according to several fishery-related factors. One of the starting points for reducing bycatch in all towed gears involves examining simple changes to the size and shape of mesh in the codend, because this is where most of the selection is believed to occur (Wileman et al., 1996). Broadhurst and Kennelly (1996) and Broadhurst et al. (2004) showed that codends made from thick twine and with large posterior circumferences, like those used conventionally by squid trawlers in Broken Bay, have very narrow lateral mesh openings and have poor selectivity. Three of the simplest methods for improving selection in codends involve 1) reducing the posterior circumference (e.g., Broadhurst and Kennelly [1996]), 2) increasing the mesh size (e.g., Reeves et al. [1992]), or 3) orienting meshes, typically orienting 60–90% of the size of the existing diamond-shaped mesh on the bar so that they are square shaped (e.g., Thorsteinsson [1992]; Broadhurst et al. [2004]).

These three modifications were tested during the present study but, with the exception of the square-mesh codend, none were demonstrated to significantly improve species selection or influence the sizes of individuals caught. The considerable temporal variability in catches and a concomitant lack of power to detect small effects may partially account for the lack of differences detected, but a more likely explanation is that the magnitude of changes to mesh openings in relation to the sizes of target and bycatch species was insufficient. Given that some small fish escaped from the square-mesh codend, future work would probably benefit from further examination of increasing codend mesh openings as a means for reducing bycatch.

In contrast to subtle modifications to codend meshes that were tested, it was demonstrated that BRDs

designed from an understanding of the behavior of fish and squid were effective in allowing fish to escape and did not significantly reduce the catches of squid. The escape of fish through these BRDs was a direct consequence of 1) their behavior and species-specific swimming abilities in the trawl (Wardle, 1983; Watson, 1989) and 2) the location of the BRDs with respect to the influences of water-flow (Broadhurst et al., 2002). More specifically, when fish enter the codend they are often herded together and herding invariably initiates movement towards the top and sides. The density of the school and any species-specific behavioral responses (Watson, 1989) determine the extent of such movement. Panels of square-shaped mesh, if strategically positioned, have been demonstrated to allow actively swimming fish to escape the trawl through the large openings in the square-shaped mesh (Broadhurst, 2000). An important contributing factor is the effect of anteriorly displaced water in front of the catch, which reduces relative flow and assists small fish to maintain their position in the codend. Broadhurst et al. (2002) demonstrated that these effects diminish with increasing distance forward and that the optimal location for BRDs designed on fish behavior is up to 1.2 m anterior to the last row of meshes in the posterior section of the codend (i.e., the position of all BRDs examined in our study).

The behavior of squid in trawls, codends, or near BRDs has not been examined in detail. Glass et al. (1999), however, observed that the reaction of schooling *L. pealeii* during initial detection of the gear was similar to fish. Individuals orientated away and then, as a result of compensatory movements in response to shifts in their visual field (termed the optomotor response), attempted to maintain position in the mouth and body of the net. After a short period, all squid were observed to stop swimming, turn, rise in the net, and fall back toward the posterior section of the trawl and toward the codend. Their behavior in this region of the net was not documented, but, given the lack of significant reductions in the catches of squid (or other cephalopods) by prawn trawls containing behaviour-based BRDs (e.g., Broadhurst et al. 2002) and the results observed in our study, active escape is probably limited.

There was a nonsignificant reduction in the weight of squid from the codends containing BRDs in experiment 1, and especially the diamond BRD, but this reduction probably occurred during retrieval of the codend. Typically, once the trawl is winched to the surface, a delay of up to three minutes can occur while the vessel is stopped, the retrieval line is connected, and the codend is brought onboard. During this period, any squid in the anterior codend or extension section may wash forward and out of the escape opening in the BRD. Watson (1989) observed similar effects during the retrieval of prawn trawls in the Gulf of Mexico and, more recently, Brewer et al. (1998) highlighted this escape route as being a major cause of loss of prawns from several BRDs in trawls used in the Gulf of Carpentaria, Australia. A simple way of minimizing the potential for such losses when using the diamond BRD would be to keep the vessel moving, thus maintaining drag on the codend, during retrieval. A simpler and more practical solution would be to substitute the square-mesh BRD with panels made from 75-mm mesh hung on the bar, since the 75-CSMP and 75-panel codends tested in Experiment 3 showed no evidence of loss of squids. Assuming that fish escaping from the CSMP survive the process (Broadhurst et al., 1997), the results presented in this study support the adoption of the CSMP codend in Broken Bay squid trawls. As a consequence of this study, and the co-operative relationship established between the NSW Department of Primary Industries and commercial fishermen, a square-mesh panel BRD has been voluntarily adopted throughout the Hawkesbury River squid-trawl fishery.

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The relationships between fish assemblages and the amount of bottom horizontal beam exposed at California oil platforms: fish habitat preferences at man-made platforms and (by inference) at natural reefs

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Abstract—Between 1995 and 2002, we surveyed fish assemblages at seven oil platforms off southern and central California using the manned research submersible *Delta*. At each platform, there is a large horizontal beam situated at or near the sea floor. In some instances, shells and sediment have buried this beam and in other instances it is partially or completely exposed. We found that fish species responded in various ways to the amount of exposure of the beam. A few species, such as blackeye goby (*Rhinogobiops nicholsii*), greenstriped rockfish (*Sebastes elongatus*), and pink seaperch (*Zalembius rosaceus*) tended to avoid the beam. However, many species that typically associate with natural rocky outcrops, such as bocaccio (*S. paucispinis*), cowcod (*S. levis*), copper (*S. caurinus*), greenblotched (*S. rosenblatti*), pinkrose (*S. simulator*) and vermilion (*S. miniatus*) rockfishes, were found most often where the beam was exposed. In particular, a group of species (e.g., bocaccio, cowcod, blue (*Sebastes mystinus*), and vermilion rockfishes) called here the "sheltering habitat" guild, lived primarily where the beam was exposed and formed a crevice. This work demonstrates that the presence of sheltering sites is important in determining the species composition of man-made reefs and, likely, natural reefs. This research also indicates that adding structures that form sheltering sites in and around decommissioned platforms will likely lead to higher densities of many species typical of hard and complex structure.

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Understanding the habitat preferences of deeper-water (below scuba depth) fishes has proven to be elusive. Off the Pacific Coast, several studies (Stein et al., 1992; Yoklavich et al., 2000; Nasby-Lucas et al., 2002) have demonstrated that habitat characteristics play a major role in shaping deeper-water fish assemblages. In those studies it was apparent that, although individuals of many species may be found in a number of habitats, most species showed distinct preferences. These studies clearly showed the role that hard structure plays for many species. How more subtle habitat characteristics, such as the presence of sheltering sites, may influence species composition was still unclear.

Between 1995 and 2002 we surveyed fish assemblages associated with southern California oil and gas platforms. Platforms may serve at least two functions for these fishes. First, the water column around many platforms serves as a nursery ground for a suite of rockfishes (*Sebastes* spp.) and other fish species, often harboring higher densities of these species than do nearby natural outcrops (Love et al., 2003). Second, platform bottoms, where the platform jacket and well pipes meet the sea floor, may harbor high densities of subadult and adult fishes. Most of these fishes are rockfishes, but lingcod (*Ophiodon elongatus*), painted greenling (*Oxylebius pictus*), and various members of the surfperch family (Embiotocidae) may also be abundant (Love et al., 1999; Love et al., 2003).

The platforms we surveyed were designed to have large, circular (1 m in diameter) horizontal beams that connect vertical and diagonal jacket elements at or near the sea floor. In some instances, these beams were buried, either by shells that had fallen from shallow parts of the jacket or by a combination of shells and fine sediment. In other instances, beams were partially exposed (full width of beam or partial width of beam was resting on the sea floor) or completely exposed (thus leaving a gap between the beam and sea floor). During our fish surveys, we noted that fishes appeared to be patchily distributed along the platform bottom and that some species seemed to be responding to the presence or absence of the beam and to the amount of space under the beam. Because the beams are all composed of similarly shaped steel and differ only in the amount of surface exposed, we hypothesized that patterns of fish associations with this structure would present insights into the role that sheltering spaces play in determining species assemblages in both natural and man-made habitats.

Materials and methods

Field sampling

Between 1996 and 2002, we surveyed fish assemblages around seven oil and gas platforms in southern and central California (Table 1, Fig. 1) using the *Delta* research submersible, a 4.6-meter, 2-person vessel, operated by Delta Oceanographics of Oxnard, California. Aboard the *Delta,* we conducted belt transects about two meters from the platform while the submersible maintained a speed of about 0.5 knots. Surveys were conducted in fall, in order to optimize good weather and water clarity.

Submersible surveys were conducted during daylight hours between one hour after sunrise and two hours before sunset. During each transect, a researcher made observations from a viewing port on the starboard side of the submersible. An externally mounted hi-8 mm video camera with lights filmed the same viewing field as seen by the observer. The researcher identified, counted, and estimated the lengths of all fishes and verbally recorded those data on the video. All fishes in a volume two meters from sea floor upwards and two meters from the submersible outwards were counted. Fish lengths were estimated by using a pair of parallel lasers mounted on either side of the external video camera. The projected reference points were 20 centimeters apart and were visible to both the observer and the video camera.

We defined the amount of beam exposure on a scale of 0–4: 0=the beam was completely covered by shells and soft sediment and it was not visible; 1=only the top of the beam (usually encrusted with invertebrates) was visible; 2=the beam was partially exposed (top and sides)—the bottom of the beam remaining in contact with the sea floor; 3=the beam was completely exposed and formed an open crevice less than 0.5 m high; and 4=the beam was completely exposed and formed an open crevice more than 0.5 m high (Fig. 2). For each fish we recorded the size of the gap with which the fish associated.

An environmental monitoring system aboard the submersible continuously recorded date, time, depth, and altitude above the sea floor of the vessel. These environmental data were overlaid on the original videotape upon completion of each survey. Transect videos were reviewed aboard the research vessel or in the laboratory and observations transcribed into a database.

Statistical analysis

We were interested in broad patterns of species' distribution among small-scale habitats. Because rare species may prefer some (nonmeasured) extreme habitat and thus potentially would have skewed a general picture, we did not use those species where fewer than 40 fish were seen or those that were not seen on at least five dives. This left us with 27 species (of the original

Table 1

Platforms, bottom depths, crossbeam exposure parameters, and numbers of fishes surveyed in this study. Beam exposure scale: 0=beam was completely covered and not visible; 1=only the top of the beam was visible; 2=the beam was partially exposed—the bottom of the beam remaining in contact with the sea floor; 3=the beam was completely exposed and formed an open crevice less than 0.5 m high; 4=the beam was completely exposed and formed an open crevice more than 0.5 m high.

Platform	Years	Depth (meters)	Amount of platform covered (0) or exposed (1–4) (length in meters, percent of total in parentheses)					Total amount of beam (covered and exposed, in meters)	Mean gap size (and standard deviation)	Number of fishes
			0	1	2	3	4			
Irene	1996–2001	73	422 (33.9)	142.2(11.4)	449.9(36.2)	229.5(18.5)	0	1243.6	1.4(0.8)	10,591
Hidalgo	1996–2001	130	146.9(9.3)	458.9(29.2)	478.1(30.2)	499.8(31.6)	0	1583.8	1.8(0.9)	11,509
Harvest	1996–2000	205	934.8(73.9)	172.9(13.7)	80.8(6.4)	76.9(6.1)	0	1265.5	0.5(0.4)	775
Hermosa	1996–2000	183	235.5(18.4)	721.3(56.4)	299(23.4)	24.2(1.9)	0	1279.9	1.1(0.6)	7195
Holly	1996–1999, 2001	64	744.4(71.0)	82.2(7.8)	82.8(7.9)	126.6(12.1)	12.7(1.2)	1048.7	0.7(0.6)	4196
Grace	1996, 1997, 1999–2002	96	512.2(32.4)	17.7(1.1)	81.3(5.1)	484.5(30.6)	486.9(30.8)	1583.1	2.3(1.3)	16,688
Gail	1996, 1997, 1999–2002	224	68.8(3.8)	4.8(0.3)	774.4(43.0)	951.4(52.9)	0	1799.5	2.5(1.1)	2045
Total			3064.5	1600.1	2246.9	2393.0	499.5	9804.1		52,999

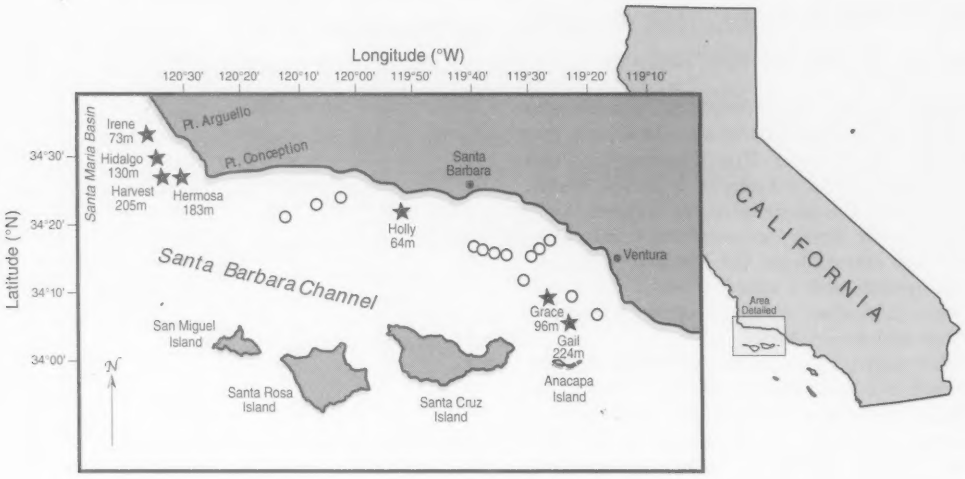

Figure 1

Location of platforms in the Santa Barbara Channel and Santa Maria Basin. Platforms discussed in this paper are shown as black stars and their bottom depths are indicated. The open circles indicate other platforms.

65) and 50,048 fish of the original 52,999 observations, or 95.1% of fish observed on all dives. In our analyses, we separated bocaccio (*Sebastes paucispinis*) and lingcod into two categories, YOY and older fishes, based on length-at-age and length-at-first-maturity data (Miller and Geibel, 1973; Cass et al., 1990; Love et al., 2002).

We used chi-square goodness-of-fit tests to determine which species tended to avoid or favor certain beam habitats. Species tend to be associated with particular depth ranges, platforms are placed at fixed depths, and some species may or may not have ever been observed on some platforms. Thus, the proportion of a particular beam habitat available to a given species was determined as the proportion of that habitat occurring only on those platforms where the species was observed. We hypothesized that if a particular species does not favor or avoids certain habitats, the expected number of those fish seen in particular habitats would be proportional to the amount of available habitat. In equation form: Let $u_{j,i}$ be the proportion of gap j (j=0, 1, 2, 3, or 4) available to species i (i=1, 2..., 27) and T_i be the total number individuals of species i observed. Then, the expected number of fish i at gap j, $E_{j,i} = u_{j,i} \times T_i$. Under the null hypothesis for species i,

$$X_i^2 = \sum_{j=0}^{4} \frac{(O_{j,i} - E_{j,i})^2}{E_{j,i}}$$

is distributed as a chi-square random variable with n_i–1 degrees of freedom, where n_i is the number of u_{ij}>0. The asymptotic assumptions for the chi-square test are not valid if the expected value of many cells is small. Cochran (1954) developed a conservative rule of thumb that the test not be used if more than 20% of the expected cell frequencies are less than five. Koehler and Larntz (1980) suggested that the chi-square test is reasonable if the total number of observations is greater than 10, the number of categories is at least 3, and the square of the number of observations is greater than 10 times the number of categories.

If the goodness-of-fit hypothesis was rejected, we examined the individual deviations, $X_{ji} = (O_{ji} - E_{ji})/(E_{ji})^{.5}$, which are approximately distributed as normal (0,1) random variables under the null hypothesis. Small values of X_{ji} indicate that the species is found less often than predicted, whereas large values indicate it is found more often.

Results

All species satisfied both the Cochran (1954) and Koehler and Larntz (1980) criteria for the validity of the chi-square test (Table 2). The null hypothesis that species are randomly distributed among the crevice habitats was rejected (P<0.0001) for all but one species, kelp greenling (*Hexagrammos decagrammus*) (Table 2).

We surveyed a total of 9804.1 m^2 of sea floor. Platforms varied both in the amount of horizontal beam exposed and, when exposed, the degree of gap between beam and sea floor. At each platform, there was relatively little annual variability in the amount of beam exposed or the size and type of gap (Fig. 3). Mean size of gap per platform over the entire study ranged from 2.5 (SD=1.1) to 0.5 m (SD=0.4). (Fig. 3, Table 1). Platforms Gail and Grace, in the east Santa Barbara Channel, had the greatest amount of gap. In particular, almost none of the bottommost beam at Gail was completely buried and most of it was at least partially exposed. At the

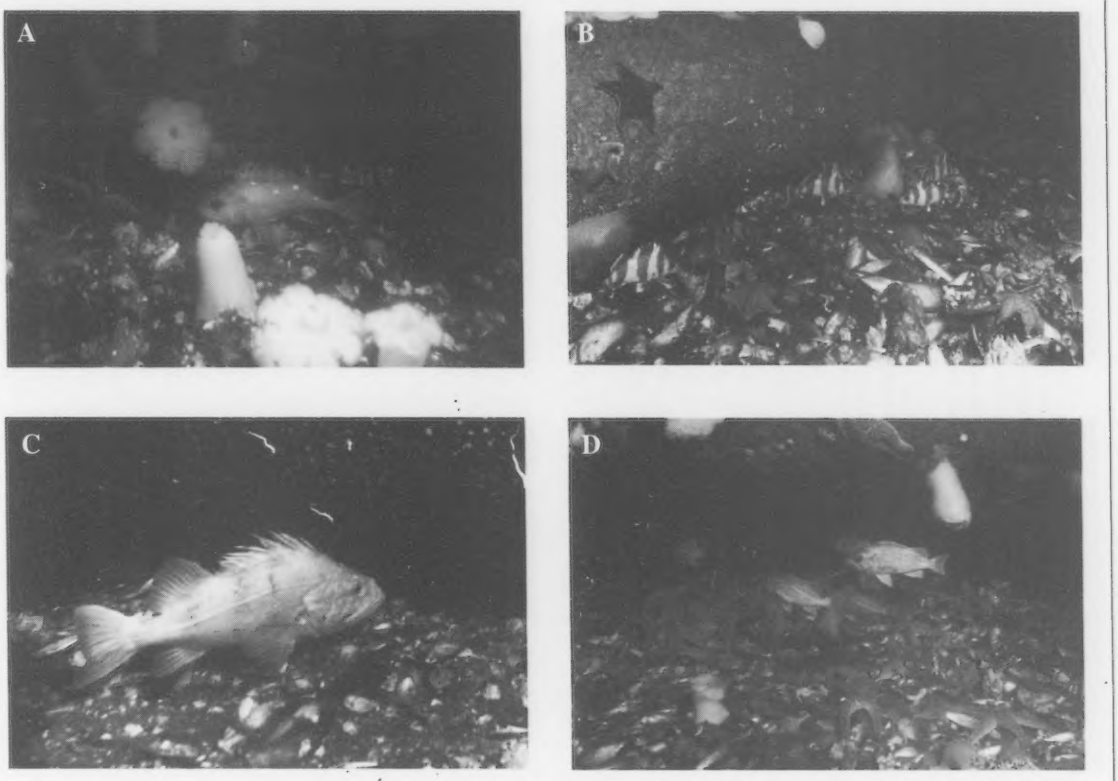

Figure 2

Examples of four types of bottom beam structure: (**A**) at least some of the beam was visible, but the full width of the beam rested on the sea floor (greenspotted rockfish, *Sebastes chlorostictus*); (**B**) the beam was partially exposed, remaining in contact with the sea floor at its bottom, not its sides (flag rockfish, *S. rubrivinctus*); (**C**) the beam was completely exposed and formed an open crevice less than 0.5 m high (cowcod, *S. levis*); (**D**) the beam was completely exposed and formed an open crevice more than 0.5 m high (vermilion rockfish, *S. miniatus*).

other extreme, most of the bottom beam at both Platforms Holly in the central Santa Barbara Channel and Harvest, off Point Conception, was completely buried. We saw little relationship between geographic location (or platform depth) and mean gap size. For instance, Platforms Hidalgo and Harvest are located within 4.6 km of each other, yet have very different beam exposures, as do Platforms Holly and Irene that are sited at almost the same depth. A lack of relationship probably reflects differences in oceanographic conditions, because some of these structures are found in areas where strong currents scour the bottom, whereas others are found in areas where sediments have not been disturbed.

Except for kelp greenling, all species exhibited some beam habitat preference (Table 2). Species found more often where the beam was completely buried (gap 0) included greenstriped (*S. elongatus*), non-YOY lingcod, rosy (*S. rosaceus*), sharpchin (*S. zacentrus*), and stripetail (*S. saxicola*) rockfishes, painted greenling, pink seaperch (*Zalembius rosaceus*), and sanddabs (*Citharichthys* spp.). Those that favored the presence of the beam or some amount of exposure (exposures 1 and 2) included calico (*S. dallii*), copper (*S. caurinus*), flag (*S. rubrivinctus*), and pinkrose (*S. simulator*) rockfishes, pile perch (*Rhacochilus vacca*), and sharpnose seaperch (*Phanerodon atripes*). Species that tended to inhabit areas where there was a gap between beam and sea floor (exposures 3 and 4) were blue (*S. mystinus*), brown (*S. auriculatus*), canary (*S. pinniger*), greenblotched (*S. rosenblatti*), halfbanded (*S. semicinctus*), squarespot (*S. hopkinsi*) and vermilion (*S. miniatus*) rockfishes, and both size classes of bocaccio (*S. paucispinis*). The vast majority of cowcod (*S. levis*) were found at beams that were scored as exposures 2 and 3. Both greenspotted rockfish (*S. chlorosticus*) and YOY lingcod appeared to prefer either soft bottom without beam exposure or beam exposure without a deep gap (exposures 1 and 2).

Table 2

The observed number of fish at each exposure value, the expected number under the null hypothesis, and the chi-square statistics of goodness of fit. Observed values are coded in the following manner: 1) "– –" if $X_{ij} < -4$; indicating that the observed value is much smaller than predicted (P=0.0001), 2) "–" if $-2 < X_{ij} < -4$; indicating that the observed value is smaller than predicted, (P=0.05), 3) "+" if $4 < X_{ji} < 2$; indicating that the observed value is larger than predicted, (P=0.05), 4) "+ +" if $X_{ji} > 4$; indicating that the observed value is much larger than predicted, P = 0.0001. Beam exposure scale: 0=beam was completely covered and not visible; 1=only the top of the beam was visible; 2=the beam was partially exposed—the bottom of the beam remaining in contact with the sea floor; 3=the beam was completely exposed and formed an open crevice less than 0.5 m high; 4=the beam was completely exposed and formed an open crevice more than 0.5 m high.

	Observed number of fish at each exposure scale value						Expected number of fish at each exposure scale level					χ^2 test of null hypothesis		
Species	0	1	2	3	4	Total	0	1	2	3	4	df	χ^2	P
Blackeye goby	64 +	1	0 –	2 –	0	67	47.6	5.2	5.3	8.1	0.8	4	19.81	<0.001
Blue rockfish	13 – –	0 – –	8 –	29	55 + +	105	45.5	6.6	16.6	22.8	13.5	4	162.99	<0.001
Bocaccio (>20 cm)	16 – –	2 – –	210 – –	458 + +	138 + +	824	229.8	87.8	205.6	247.2	53.7	4	595.27	<0.001
Bocaccio (yoy)	11 – –	5 – –	8 – –	205 + +	0	229	57.1	38.3	58.1	62.1	13.4	4	451.43	<0.001
Brown rockfish	23	6	30	57 + +	0	116	59.0	11.4	27.0	18.0	0.6	4	109.81	<0.001
Calico rockfish	444 – –	168 + +	379 + +	112 – –	4	1107	563.3	108.4	257.2	172.0	6.1	4	137.34	<0.001
Canary rockfish	9 –	15	24	42 + +	4	94	28.7	19.8	19.4	19.0	7.0	4	44.80	<0.001
Copper rockfish	460 – –	192 + +	530 + +	296	3 – –	1481	641.5	92.5	234.8	321.3	190.9	4	716.18	<0.001
Cowcod	9 –	0 –	26 +	31 +	0	66	20.2	13.6	16.2	15.9	0.0	4	40.2	<0.001
Flag rockfish	88 – –	42 –	195 + +	134	12	471	147.2	76.9	107.9	115.0	24.0	4	119.00	<0.001
Greenblotched rockfish	49 – –	23 – –	304 + +	181 +	0	557	140.7	102.0	127.1	151.0	36.1	4	409.20	<0.001
Greenspotted rockfish	120 + +	329 + +	656 + +	243 – –	13 – –	1361	425.4	222.1	311.9	332.2	69.3	4	719.98	<0.001
Greenstriped rockfish	130 + +	67	84	54 –	0	335	78.3	76.7	92.2	87.7	0.0	3	49.04	<0.001
Halfbanded rockfish	4457 – –	7338	3142 – –	15,838 + +	5593 + +	36,368	13,610.8	7247.9	6690.1	6549.6	2269.6	4	26,078.39	<0.001
Kelp greenling	14	8	8	8	4	42	14.0	5.4	8.4	10.3	3.8	4	1.80	0.772
Lingcod (>20 cm)	128 +	26 –	91	88	8	341	106.6	55.7	78.2	83.2	17.4	4	27.54	<0.001
Lingcod (yoy)	201 + +	54	111 + +	16 – –	2 – –	384	143.7	76.5	70.6	69.2	24.0	4	113.52	<0.001
Painted greenling	104 + +	38 +	50	37 – –	5 –	234	61.1	22.8	60.2	73.9	16.1	4	68.19	<0.001
Pile perch	29 – –	45 + +	41	37 +	0	152	77.3	14.9	35.3	23.6	0.8	3	100.52	<0.001
Pinkrose rockfish	5 – –	11 – –	182 + +	47	0	245	69.9	50.7	65.1	59.3	0.0	3	303.86	<0.001
Pink seaperch	60 + +	1 –	6	4 –	3 –	74	28.2	15.5	8.8	12.0	9.4	4	59.99	<0.001
Rosy rockfish	61 +	12	19	29	3 –	124	41.5	15.9	24.8	30.4	11.3	4	17.74	<0.001
Sharpchin rockfish	42 + +	14	5 –	0 –	0	61	14.3	14.0	16.8	16.0	0.0	3	78.22	<0.001
Sharpnose seaperch	7 – –	205 + +	168 + +	31 – –	0	411	209.1	40.2	95.5	63.8	2.3	4	944.19	<0.001
Squarespot rockfish	186	4 – –	54 – –	237 + +	21 –	502	167.9	64.5	100.5	123.3	45.9	4	198.65	<0.001
Stripetail rockfish	197 + +	37 –	65 + +	152	0	451	111.6	61.8	129.4	148.3	0.0	3	107.37	<0.001
Unidentified sanddab	76 + +	0 –	0 –	2 – –	2 –	80	26.4	4.5	15.0	20.2	13.8	4	138.96	<0.001
Vermilion rockfish	230 – –	162 – –	525 + +	582 + +	437 + +	1936	647.4	248.6	387.5	475.4	177.2	4	753.15	<0.001
Widow rockfish	1295	53 – –	68 – –	466 –	87 –	1969	491.1	329.1	499.5	534.1	115.2	4	1935.80	<0.001

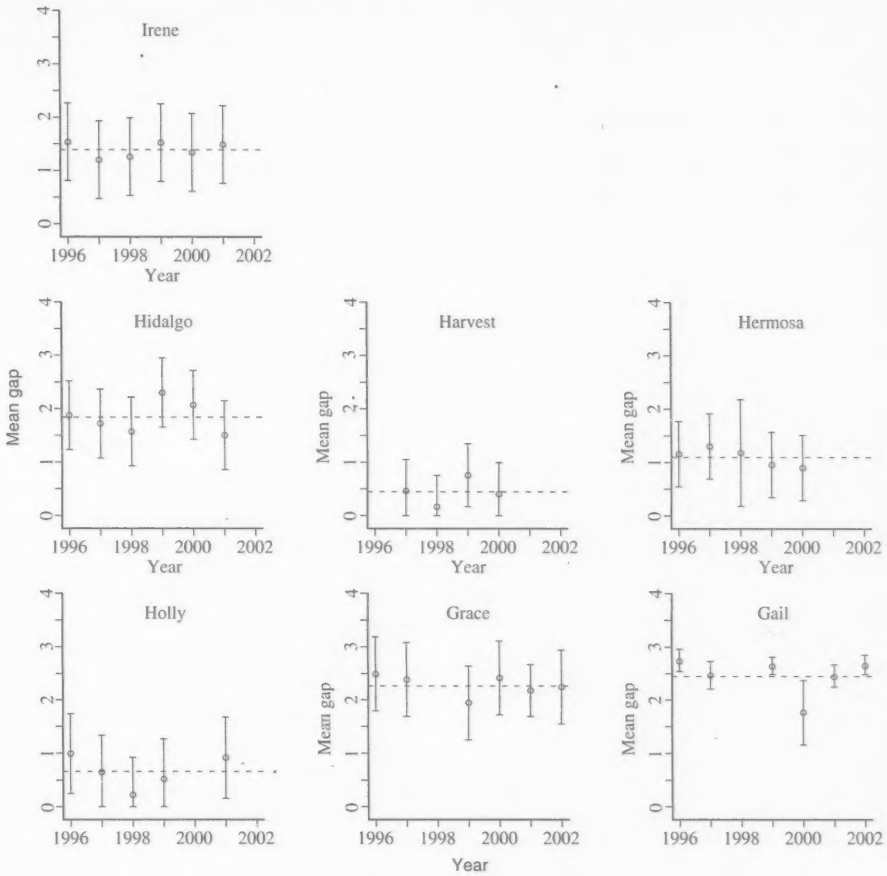

Figure 3

Mean size of gap between beam and sea floor on a scale of 0–4 at each platform, by year. Platforms are ordered from northernmost to southernmost. 0=beam was completely covered and not visible; 1=only the top of the beam was visible; 2=the beam was partially exposed—the bottom of the beam remaining in contact with the sea floor; 3=the beam was completely exposed and formed an open crevice less than 0.5 m high; 4=the beam was completely exposed and formed an open crevice more than 0.5 m high.

Many species appeared to avoid certain beam configurations; that is, they were found in numbers far less than expected by chance. For instance, blue, flag, greenblotched, halfbanded, pinkrose, squarespot, and vermilion rockfishes, and bocaccio were all significantly less abundant in areas with either no horizontal beam or where that structure was not well exposed (exposures 0 and 1). On the other hand, a variety of taxa, such as greenspotted rockfish, YOY lingcod, painted greenling, and sanddabs were relatively uncommon where there was a large gap between the bottom of the beam and the sea floor (exposure 4). Widow rockfish (*S. entomelas*), in our study comprising almost entirely YOY individuals, tended to avoid areas where the beam was exposed. Calico and copper rockfish, along with sharpnose seaperch, tended to avoid both sea floors with no beam present and sea floors where the beam structure was completely exposed (and the gap was significant).

Discussion

Species generally occupied those parts of the beams that appear to be most similar to their natural habitats (Feder et al., 1974; Yoklavich et al., 2000, 2002; Love et al., 2002). In our system, there was a suite of species that were less abundant or nearly absent when the beam was exposed. These species included blackeye goby

(*Rhinogobiops nicholsii*), greenstriped, sharpchin, and stripetail rockfishes, painted greenling, pink seaperch, and sanddabs. These species are usually referred to as "soft substrata" or "mixed substrata" fishes. Other taxa were associated more often or almost exclusively with the exposed beam and these are species often categorized in the literature as "reef" species. These included blue, brown, calico, canary, copper, flag, greenblotched, halfbanded, pinkrose, squarespot, and vermilion rockfishes, cowcod, bocaccio, pile perch, and sharpnose seaperch. As in natural systems, to a great extent greenspotted rockfishes and non-YOY lingcod inhabited several different habitats.

There is evidence that the crevices, cracks, and caves on both natural and human-made structures, may influence fish species assemblages because they form shelters for fishes (Luckhurst and Luckhurst, 1978; Kellison and Sedberry, 1998; Rilov and Benayahu, 1998). In many instances, overall fish abundances are positively correlated with these openings that enhance habitat complexity. On the Pacific Coast, there are only a few observations specifically addressing shelter sites and deeper-water fishes. Caselle et al. (2002), surveying oilfield debris off southern California, examined the influence that structural complexity may exert on fish assemblages. They found that the presence of shelter was one of the most important determinants for high densities of both copper and vermilion rockfishes and played some role in the abundance of a number of other species. Yoklavich et al. (2000) noted that the "rock habitat guild," composed of such species as cowcod, pygmy (*S. wilsoni*), and yelloweye rockfishes, were "closely associated with ledges, caves, crevices, and overhangs." Discussing yelloweye rockfish habitat off southeastern Alaska, O'Connell and Carlile (1993) stated that the "occurrence of refuge spaces may be one key to the presence of yelloweye rockfish, which were normally found in areas where refuge spaces were available, even if the surrounding habitat was not their preferred habitat of boulder or broken rock."

From our research, it was apparent that, among the reef species, there is a "sheltering" guild. These are species (i.e., blue, canary, flag, greenblotched, halfbanded, pinkrose, and vermilion rockfishes, cowcod, and bocaccio) for which an exposed beam alone is not sufficient. These taxa tend to be associated with the spaces that provide shelter under that structure. Blue, brown, canary, halfbanded, and vermillion rockfishes and bocaccio were found in particularly large numbers where the gap between beam and sea floor was largest (exposures 3 and 4). A few species, such as calico, copper, greenspotted, and pinkrose rockfishes, YOY lingcod, and sharpnose seaperch, although often found along the beams, seemed to avoid the most exposed sections.

Fishes that either avoided the beam, or at least that part that formed a gap between the beam and the sea floor, tended to be small in size and to fall into several categories. One group, the sanddabs, is adapted to living on soft substrata. Other species, including blackeye goby, greenstriped, rosy, and sharpchin rockfishes, painted greenling, and pink seaperch, are diminutive and solitary. Although pink seaperch are found in schools over natural outcrops, we did not see them schooling around platforms. All of these diminutive forms will live in high relief, complex substrata when larger predators have been removed from the system, as occurs on most of the rocky outcrops off southern and central California (M. Love, unpubl. data). However, it is likely they avoid exposed beams because of the presence in the area of high densities of large fishes.

Variability in habitat complexity, caused by variation in the amount of beam exposure and the size of gap between beam and sea floor, may explain at least one of the between-platform differences we have observed in fish assemblages. In general, platforms occupying similar depths harbor similar fish assemblages (Love et al., 2003). However, an exception was found when comparing fish species at Platform Gail (224 m) and at Platform Harvest (205 m) (Love et al., 2003). In order of density, greenblotched rockfish, bocaccio, greenspotted, stripetail, and pinkrose rockfishes dominated the bottom fish assemblage at Platform Gail. Cowcod, although not among the top five most abundant fish, were found at higher densities at this platform than at any natural outcrops or other platform that we surveyed in southern California. By contrast, at Platform Harvest, stripetail, greenstriped, greenspotted, greenblotched, and sharpchin rockfishes were most commonly seen. Cowcod were considerably less abundant at this platform and we observed almost no bocaccio. Platform Gail contains, on average, the highest mean exposure value (about 2.5 m) and Harvest the lowest (slightly more than 1.0 m). Most of the common fishes at Gail are representative of complex habitat, those at Harvest of lower relief and softer substrata.

This research may have a bearing on the ultimate disposition of California platforms. The possibility of enhancing fish habitats and fish populations at platforms is an important issue in the decommissioning process. In particular, the California Department of Fish and Game has suggested increasing habitat complexity around the bottom of platform jackets by placing quarry rock or other materials around the jacket (Schroeder and Love, 2004). However, to date, augmentation has not been attempted. With the results from our study, we predict that increasing the habitat complexity at platforms will, in some instances, increase the densities of a number of rock or boulder-oriented species, those species that are preferentially found where there is a gap below the bottom beam.

In addition, the results of this research may also be applied to natural reef studies, particularly those involving marine protected areas (MPAs). This research clearly demonstrates that, in terms of habitat preferences of many fish species, not all hard habitat is the same. In fact, this research indicates that it may be possible to predict which species are found around different types of hard structure by the presence

of different types of shelters at the hard structure. This would be particularly important when deciding on what habitats to set aside for MPAs designed to protect and enhance the populations of specific fish species.

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A Bayesian method for identification of stock mixtures from molecular marker data

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Abstract—Molecular markers have been demonstrated to be useful for the estimation of stock mixture proportions where the origin of individuals is determined from baseline samples. Bayesian statistical methods are widely recognized as providing a preferable strategy for such analyses. In general, Bayesian estimation is based on standard latent class models using data augmentation through Markov chain Monte Carlo techniques. In this study, we introduce a novel approach based on recent developments in the estimation of genetic population structure. Our strategy combines analytical integration with stochastic optimization to identify stock mixtures. An important enhancement over previous methods is the possibility of appropriately handling data where only partial baseline sample information is available. We address the potential use of nonmolecular, auxiliary biological information in our Bayesian model.

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Stock mixture analysis using multilocus genotypes of fish is recognized as a versatile tool in fisheries management. The efficiency of combining polymorphic molecular markers, such as microsatellites, with a model-based approach to estimate stock mixtures, has been clearly demonstrated in the literature (Kalinowski, 2004; Reynolds and Templin, 2004). Since the beginning of the 21st century, Bayesian methods have largely replaced the earlier applied maximum likelihood approach based on latent class mixture models (Pella and Masuda, 2001). A similar trend has been true for the estimation of genetic population structure in general (e.g., Pritchard et al., 2000; Corander et al., 2003, 2004; Beaumont and Rannala, 2004). For an earlier approach to mixture analysis with incomplete information about source populations, see Smouse et al. (1990).

Bayesian methods for estimation of stock mixtures has generally been based on exploitation of data augmentation through Markov chain Monte Carlo (MCMC), where latent origins of caught individuals and values of the other model parameters are successively simulated from the corresponding posterior distributions. Such an approach is capable of avoiding certain estimation problems caused by missing data and rare alleles, which severely affect the maximum likelihood method. However, because of numerical deficiencies, there are situations where the MCMC based method for the latent class mixture model may easily fail to provide appropriate estimates. First, in the presence of very small groups of individuals representing some stock sources, the posterior distribution of the origins for these particular individuals and the corresponding posteriors of the source allele frequencies will typically comprise a high level of uncertainty. Consequently, the resulting MCMC simulation error in the estimates may be considerable. Second, when there are baseline samples available only for a subset of potential stock sources, estimation of origins is not feasible (Pella and Masuda, 2001). Use of the standard approach with a fixed number of sources, based on the available baseline samples, may easily lead to spurious estimates when there are individuals representing several additional sources in the data. Similarly, it is difficult to detect outlier individuals with the latent class approach with a fixed number of sources (Pritchard et al., 2000) because they are unlikely to be identified in the MCMC simulation for data sets of moderate to large size. Third, under partial baseline information, it is difficult to appropriately infer a suitable number of stock sources to represent a particular data set.

Partition-based Bayesian alternatives to latent class models for identification of genetic mixtures without baseline samples have recently been introduced (Dawson and Belkhir 2001; Corander et al., 2003, 2004). Corander et al. (2003, 2004) used an analytical integration strategy combined with stochastic search methods to make Bayesian estimation

more feasible when the number of genetically diverged sources contributing to the observed data is unknown. A wide variety of applications of this approach can be found in the literature (e.g., Heuertz et al., 2004, Seppä et al., 2004, Mäki-Petäys et al., 2005). The approach by Dawson and Belkhir (2001) is similar to that of Corander et al. (2004) in spirit; however, it is subject to two important limitations that prevent an efficient use of this approach in the current context. First, there are no readily available informative forms of the family of prior distributions used by Dawson and Belkhir (2001), which would be necessary for representing the baseline information. Second, their model formulation does not allow for missing alleles in the molecular marker data, which are present in most real data sets.

In our study, we extend the partition-based approach to incorporate *a priori* baseline information, making it suitable for identification of stock mixtures, either under complete or partial baseline sample information. Our focus is on the identification of the putative genetic mixture in the catch sample data, provided by the maximum *a posteriori* estimate of the assignment of the individuals into an unknown number of sources. Given the estimate, the proportions of the stocks in the population can be readily inferred by using the standard multinomial-Dirichlet model (e.g., Pella and Masuda, 2001) and generic Bayesian software, such as BUGS (Spiegelhalter et al., 2003), which has been widely used for fish population modeling (e.g., Meyer and Millar, 1999; Mäntyniemi and Romakkaniemi, 2002; Mäntyniemi et al., 2005).

Another novelty in our method is the possibility of using available biologically relevant information to preassign catch data into groups that can be considered as sampling units in the model. For instance, when the behavior of the investigated species is such that individuals obtained simultaneously at a single catch location are known to represent the same (yet unknown) stock, they can be allocated as a single unit to an origin. Such use of auxiliary information enhances the statistical power to detect the correct origin when the number of molecular marker loci available is limited. To illustrate our modeling approach, and to investigate its performance under various biological settings, we present results from several simulation experiments based partly on real molecular data for the Baltic Sea stock mixture of Atlantic salmon (*Salmo salar*).

Methods

Bayesian stock mixture model

In stock mixture estimation, there are typically available in samples two types of individuals, which are genotyped. One type consists of individuals with known origin (baseline data), and the other type represents a catch sample, which may have been pooled from several sources. Let m be the number of potential stocks, such that for each stock $i = 1,..., m$, there are n_i baseline individuals available. Furthermore, there may be an additional number of potential stocks contributing to the catch population; however, these are not represented by any baseline samples. We let K ($m \leq K$) denote the total number of potential stocks, which can have contributed to a catch sample of n individuals, whose origins are unknown. Notice that K is typically determined from the relevant biological information about the species under consideration. The target for our estimation is to infer the number of stocks, say k, having actually contributed to the catch sample, from the multilocus genotypes of both the baseline and catch individuals.

Under the assumption that the genetic information consists of N_L molecular marker loci, where at each locus $j = 1,..., N_L$, there are $N_{A(j)}$ different alleles distinguished among all baseline and catch samples. Pella and Masuda (2001) introduced a rather complicated empirical Bayes procedure to determine the prior distribution for the allele frequencies in the potential stocks through the observed genotypes of the baseline individuals (all stocks were assumed to be represented by baseline samples). Here we consider a simpler approach, by suitably modifying the standard Dirichlet prior used in Corander et al. (2003, 2004). We assume that the allele frequencies between marker loci are conditionally independent given the stock origins and consider the potential stocks to be in Hardy-Weinberg equilibrium (HWE).

Let p_{ijl} be the unknown frequency (or probability) of allele l in the stock i at locus j, given that k ($k \leq K$) stocks are considered. Further, for each locus $j = 1,..., N_L$, let α_{ijl} be a hyperparameter for a Dirichlet prior distribution of the allele frequencies of stock i ($i = 1,..., k; l = 1,..., N_{A(j)}$). Given the baseline information, we may partially update our beliefs about the allele frequencies using the posterior distribution derived from an initially vague reference prior. For each of the m stocks, where baseline samples are available, we set $\alpha_{ijl} = n_{ijl} + 1/N_{A(j)}$, where n_{ijl} is the observed number of copies of allele l at locus j among individuals in the baseline sample of size n_i. This hyperparameter updating procedure is standard in Bayesian analysis with the multinomial-Dirichlet model (Gelman et al., 2004). Correspondingly, for the other potential stocks, not represented by any baseline information, the count n_{ijl} is zero, and the hyperparameter is determined as $\alpha_{ijl} = 1/N_{A(j)}$.

A putative assignment of the catch data to the potential stocks is represented in our study by a partition-valued parameter $S = (s_1,..., s_k)$, which allocates the n individuals into k non-empty clusters. A cluster is labeled as either the corresponding baseline sample or, alternatively, as a group of unknown geographical origin. The prior distribution of the allocation parameter $P(S)$ is defined according to

$$P(S = (s_1,..., s_k)) = \begin{cases} c, \text{ if } k \leq K \\ 0, \text{ otherwise} \end{cases}, \quad (1)$$

which corresponds to a uniform distribution over the possible allocations of the catch individuals under the

restriction $k \leq K$. This particular prior specification allows a convenient estimation algorithm to be constructed for identifying those allocations associated with high posterior probabilities, given the molecular marker data. Also, our prior is considerably more informative from the biological perspective than the uniform prior with $K = n$ used in Corander et al. (2004) because it assigns a zero probability to most allocations that are very unrealistic for a moderate or large sample size n.

The posterior probability of an allocation S over the class of all putative candidates is defined as

$$p(S \mid data) = p(data \mid S)P(S) / \sum_{S \in \Im} p(data \mid S)P(S), \quad (2)$$

where $p(data|S)$ is the marginal likelihood of having the allele frequency parameters of each class s_i in S integrated out analytically (formula A1 in Corander et al., 2003) according to

$$p(data \mid S) = \prod_{i=1}^{k} \prod_{j=1}^{N_L} \left[\frac{\Gamma(\sum_l \alpha_{ijl})}{\Gamma(\sum_l \alpha_{ijl} + n_{ijl})} \prod_{l=1}^{N_{Al,j}} \frac{\Gamma(\alpha_{ijl} + n_{ijl})}{\Gamma(\alpha_{ijl})} \right], \quad (3)$$

where n_{ijl} is now the observed number of copies of allele l at locus j among catch individuals allocated to cluster i. The analytical integration approach was used earlier in a related genetic context by Balding and Nichols (1997), Rannala and Hartigan (1996), Rannala and Mountain (1997).

As can be seen from the above expression, the parameter that needs to be estimated in our stock mixture model is the allocation partition S. In situations where auxiliary biological information provides a pre-assignment of some catch individuals into *a priori* sampling units, each known to represent a single unknown origin, the above formula still applies. However, the prior distribution of the allocation parameter needs to be modified accordingly, to exclude the values of S that assign individuals in the same sampling unit to distinct origins.

Algorithm for allocation estimation

In the sequel, we consider the general situation where the catch data are represented by a number of *a priori* sampling units, each containing potentially more than a single individual (see the previous section). When no auxiliary information for pre-assignment to sampling units is available, each sampling unit will correspond to a single individual in the catch data.

The two main aspects of our stock mixture model that need to be estimated from marker data are the number of clusters (k) suitable for a particular data set, and the allocation of sampling units to the clusters. Corander et al. (2003, 2004) used various stochastic search strategies for estimation of a comparable model without prior baseline samples. In our study, we develop an alternative method to enable analyses of data sets ranging from moderate to challenging because the MCMC algorithms introduced by Corander et al. (2003, 2004) are computationally time and memory intensive. The central idea is to use a "greedy" stochastic search algorithm (Fletcher, 1987) to find a partition S with the highest posterior probability (Eq. 2). Repeated runs of the algorithm enable investigation of the stability of the estimation procedure, in a way that is similar to the parallel MCMC approach of Corander et al. (2004).

An initial partition for the algorithm is determined by assigning sampling units one by one to such a cluster, so that the resulting partition has the highest possible posterior probability. After specifying the initial partition, the greedy algorithm proceeds by performing the following operations repeatedly on the current partition:

1 The algorithm moves sampling units from one cluster to another. In a stochastic order, for each sampling unit, it calculates the change imposed to the posterior probability $P(S|data)$ by moving the particular sampling unit to any of the other clusters, including even an empty cluster, unless that would lead to $k > K$. It moves the sampling unit to the cluster that increases the value of $P(S|data)$ most (if no increase is possible, the sampling unit is not moved).
2 It joins clusters. For each pair of clusters, the algorithm calculates the change to $P(S|data)$ imposed by joining them. It joins the two clusters that cause the maximal increase (if no increase is possible, no clusters are joined).
3 It splits clusters. Using the Kullback-Leibler divergence between sampling units (Corander et al., 2003), the algorithm splits each cluster into maximally 20 subclusters and calculates the change to $P(S|data)$ imposed by keeping one of the introduced subclusters as a separate new cluster, or by joining it to any of the previously existing clusters. It keeps the new configuration that improves the value of $P(S|data)$ most (if no improvement is possible the split is not made).
4 It splits clusters into exactly two maximally homogeneous subclusters with the Kullback-Leibler divergence, otherwise analogously as in step 3.
5 It re-allocates several sampling units from a cluster. In a stochastic order, for each cluster, the algorithm orders the sampling units of the cluster such that the first sampling unit is the one whose removal from the cluster would improve the marginal likelihood of the cluster most, and so on. A putative candidate for a new partition is formed by moving sampling units one by one to some other cluster, such that the $P(S|data)$ of the resulting partition is as high as possible (these moves are performed even if a single move results in a worse solution). If at some point the total change in $P(S|data)$ is positive, the putative candidate is accepted and operation 5 is completed. When the total change remains negative, even after re-allocation of all the sampling units in a single cluster, the putative candidate is rejected and another cluster is chosen as a target until all clusters have been considered.

The optimization operations are repeated in a varying order, until none of them improves the posterior probability $P(S|data)$ of the current partition. The allocation of sampling units to different clusters is based on the obtained partition, and the suitable number of clusters k is estimated from the partitions visited during the simulation.

Measurement of the strength of evidence for any particular value of the partition S, given the marker data, is an intricate process, in particular for large data sets from complex stock mixtures. Theoretically, the unknown largest posterior probability may be extremely small, even in situations where a particular model provides an adequate fit to the observations. An important factor explaining such a feature is the large number of possible allocations, which all have positive posterior probabilities by definition. This feature is of general concern in a Bayesian analysis that comprises vast model spaces, see, e.g., the discussion in Madigan and Raftery (1994). Because the actual estimated value of the posterior probability may be an intuitively misleading goodness-of-fit measure, we use an alternative strategy for characterization of the uncertainty in relation to the estimated allocation.

Bayes factors (e.g., Kass and Raftery, 1995) provide a computationally efficient approach to local assessment of the amount of the peak of the posterior distribution around an estimate of S. Let S^* denote an alternative allocation obtained from an estimate S by moving any particular sampling unit to another putative stock. The strength of evidence in favor of placing that sampling unit in the original stock against placement in the new stock is provided by the Bayes factor

$$B_{S,S^*} = \frac{p(data \mid S)P(S)}{p(data \mid S^*)P(S^*)}, \quad (4)$$

which measures how many times more plausible the allocation S is for the particular sampling unit. When the value of Equation 4 is small, say $B_{S,S^*} < 10$ (or $\log_e B_{S,S^*} < 2.3$, Kass and Raftery, 1995), the data do not strongly support a single origin for the particular sampling unit. Because calculation of these Bayes factors is computationally inexpensive, they can be easily provided for every possible sampling unit or stock combination.

In addition to Bayes factors, conditional posterior probabilities for the allocation of each individual over the range of different putative stocks identified through S can be used to characterize the uncertainties in the Bayesian estimate. The conditional posterior probability distribution is defined for each individual by

$$P(S_i \mid data) = \frac{p(data \mid S_i)P(S_i)}{\sum_{i=1}^{k} p(data \mid S_i)P(S_i)}, \quad (5)$$

where S_i denotes that the particular individual is allocated to the ith class of S (over the k possible alternatives). When only a single stock has a high conditional posterior probability, the allocation is made on a firm basis. However, when at least two sources are identified with reasonably high posterior probabilities, the genetic evidence is not conclusive enough for a classification of the particular individual to a single source. The advantage of the conditional posterior probabilities over Bayes factors in characterization of the classification uncertainty for each individual is that the former compares simultaneously all putative sources, whereas the latter provides only a pairwise judgement.

The correct number of clusters needed to describe the data can be estimated from the partitions that were visited during the simulation. During the simulation the algorithm stores the marginal likelihoods and the sizes of the 30 best visited partitions, and the posterior probabilities for the different numbers of clusters can then be estimated analogously to those estimated by Corander et al. (2004). Usually, if there is a lot of molecular data available (e.g., hundreds of loci have been observed) only a few of the best partitions have influence on the computed posterior probabilities because the relation of marginal likelihoods between different partitions can be up to ~exp(1000). If the data are sparse (e.g., only about 10–20 loci have been observed) and only partial baseline information is available, the uncertainty related to the correct number of clusters can be considerable because many partitions with differing sizes and approximately equal marginal likelihood may be found. In these cases, to obtain a more reliable estimate of the correct number of clusters, the algorithm should be run multiple times with different upper bounds (K) in order to facilitate the identification of those partitions that have real influence in the posterior probabilities. In our implementation of the estimation algorithm, we have included the possibility to automatically process information from multiple runs.

Empirical illustration of the partition-based approach

The Bayesian estimation algorithm described in the previous section is implemented in BAPS software.[1] The examples considered here are produced by BAPS analyses of data simulated by using the real data from Koljonen et al. (2002), who assessed allele frequencies for nine microsatellite markers in Atlantic salmon within the Baltic Sea region. We have experimented with several simulation configurations to investigate how our method would be expected to perform under a variety of biological conditions.

The five wild stocks of Atlantic salmon considered in Koljonen et al. (2002) correspond to five different rivers draining into the Baltic Sea: Tornionjoki (TornW), Simojoki (Simo), Iijoki (Ii), Oulujoki (Oulu), and Neva. The pairwise genetic distances (Nei's D_A, Nei et al., 1983) between these stocks underlying our simulations are

[1] BAPS software is freely available at URL http://www.rni.helsinki.fi/~jic/bapspage.html. Results presented here were calculated with version 3.1 (release date 5 March 2005).

given in Table 1 (reproduced from Koljonen et al., 2002). An estimate of total F_{ST} (Weir and Cockerham, 1984) equal to 0.07 was obtained in Koljonen et al. (2002) for these stocks on the basis of the nine microsatellite loci. The magnitude of the genetic differentiation in the underlying population is fairly small, and the pairwise distances vary considerably. Thus, we may conclude that these stocks represent a biologically challenging setting for inference about the genetic mixture in a population sample. Using the individual stock allele frequencies, we have simulated baseline individuals and catch samples under the assumptions of HWE and no linkage between the loci. A wide variety of configurations, with complete and partial baseline information and different sample sizes, were tested. In the analyses involving five underlying stocks, we used $K = 10$ as the prior upper bound, and the estimation algorithm was run 12 times for each replicate data set. For cases with only two underlying stocks, the upper bound was set as $K = 6$.

Results of our simulation experiments are summarized in Tables 2–8. As a summary, we highlight the following aspects. Uneven proportions of stock presence in the samples do not seem to affect the inference notably, even when the baseline information is only partial. The results in Table 3 are produced under a particularly challenging situation, where the baseline information comprises 40 individuals from a single stock only. The sample configuration then contains 40 individuals from this stock and 10 individuals from another, *a priori* unknown stock. The results show that our method performs surprisingly well in the identification of the outgroup, given that the genetic difference between the two underlying stocks is not negligible. However, as the results in Table 4 illustrate, the presence of putative stocks not represented by baseline information may also be masked by the baseline available for a genetically similar stock. Identification of putative stocks without using any baseline information may *de facto* be more successful under such circumstances (compare Tables 4a–4d). Therefore, we suggest that in practice both types of analyses are performed and the results compared, since this is computationally inexpensive with our method. Our results indicate that incomplete baseline information is expected to be most fruitful for the identification task when there are baseline samples available from the stocks that are genetically most similar. The baseline configurations in Table 4 can be

Table 1

Pairwise genetic distances (Nei's D_A, Nei et al., 1983) between different Atlantic salmon stocks within the Baltic Sea region (reproduced from Table 2 in Koljonen et al., 2002). Stocks correspond to five different rivers: Tornionjoki (TornW), Simojoki (Simo), Iijoki (Ii), Oulujoki (Oulu), and Neva.

Stocks	TornW	Simo	Ii	Oulu
Simo	0.129			
Ii	0.068	0.125		
Oulu	0.110	0.164	0.131	
Neva	0.261	0.285	0.284	0.261

Table 2

Allocation average percentages over 20 simulations, when 25 individuals from each stock were present in the sample data, and the number of baseline individuals available from each stock was (**A**) 30, (**B**) 15, and (**C**) 5. The column with the heading "Other" refers to additional stocks inferred by the method. Stocks correspond to five different rivers: Tornionjoki (TornW), Simojoki (Simo), Iijoki (Ii), Oulujoki (Oulu), and Neva.

		Allocation					
Origin		TornW	Simo	Ii	Oulu	Neva	Other
A	TornW	0.80	0.01	0.15	0.03	0.00	0.00
	Simo	0.03	0.95	0.02	0.00	0.00	0.00
	Ii	0.11	0.02	0.84	0.03	0.00	0.00
	Oulu	0.03	0.01	0.01	0.95	0.00	0.00
	Neva	0.00	0.00	0.00	0.00	1.00	0.00
B	TornW	0.72	0.03	0.18	0.06	0.00	0.00
	Simo	0.02	0.94	0.02	0.02	0.00	0.00
	Ii	0.11	0.03	0.84	0.02	0.00	0.00
	Oulu	0.04	0.01	0.03	0.91	0.00	0.00
	Neva	0.00	0.00	0.00	0.00	0.99	0.00
C	TornW	0.59	0.06	0.23	0.09	0.01	0.02
	Simo	0.04	0.90	0.04	0.01	0.00	0.00
	Ii	0.20	0.06	0.70	0.03	0.00	0.01
	Oulu	0.03	0.01	0.05	0.91	0.00	0.00
	Neva	0.00	0.00	0.00	0.00	0.98	0.02

Table 3

Origin identification performance when the sample consists of 40 individuals from the Iijoki River (Ii) and 10 individuals from another stock. Stocks correspond to five different rivers: Tornionjoki (TornW), Simojoki (Simo), Iijoki (Ii), Oulujoki (Oulu), and Neva.Baseline information was in each case available only from Ii (40 simulated individuals). The numbers are based on 50 replicates of each configuration.

Stock without baseline (outgroup)	Percentage of correct recognition for individuals from Ii			Percentage of correct recognition for individuals from the outgroup			Percentage of replicates where at least 50% of the outgroup was recognized
	min.	max.	avg.	min.	max.	avg.	
Neva	0.95	1.00	0.9955	0.9	1.00	0.998	1.00
Oulu	0.875	1.00	0.9665	0.0	1.00	0.7440	0.86
Simo	0.85	1.00	0.9705	0.0	1.00	0.6820	0.90
TornW	0.90	1.00	0.9820	0.0	0.80	0.3660	0.34

categorized in this respect as neutral (no biasing effect; Table 4, A and B), positive (strengthens the inference; Table 4C), negative (biases the inference; Table 4, D and E).

Our results indicate that commonly occurring levels (<5%) of missing marker data do not inhibit the ability of our method to detect the correct stocks, assuming that the missing values are randomly distributed over loci and individuals (Table 5). As an overall conclusion from the simulations, it is clear that the genetic dissimilarities of the stocks matter most for identification performance. When baseline samples are available for all stocks, most individuals can be correctly assigned to their origin even when the genetic distance between the stocks is negligible (such as between Tornionjoki and Iijoki rivers). Usefulness of the conditional posterior probabilities for characterization of the allocation uncertainty is exemplified in Table 6.

The number of inferred putative stocks was in general well in accordance with the underlying true number and there was no tendency to overestimate k. However, when the number of available marker loci was decreased to five (Table 7), the probability of obtaining additional putative stocks was slightly increased. Because it is widely known that the level of polymorphism of the markers affects their usefulness in origin identification, it is difficult to specify very clear boundaries with respect to the amount of loci necessary for an acceptable performance of any assignment method. It is important to notice that an acceptable characterization of uncertainty inherently depends on the real biological context in a particular modeling situation. As a simple rule of thumb for our method, we would suggest that $N_L \leq 6$ might be regarded as an insufficient value for reliable estimation. However, when auxiliary information is available such that the sample data can be grouped before analysis (as in Table 8), the statistical power to detect correct origins and k increases considerably. This situation would correspond to a geographical sampling scheme where the individuals assigned to the same sampling unit are caught simultaneously at a specific location.

Discussion

We have introduced a novel Bayesian method for an investigation of stock mixtures using molecular marker data by suitably modifying existing partition-based Bayesian models for estimation of genetic population structure. To enable smooth applicability, the implementation is made freely available in a user-friendly software. One particular advantage of our method is the possibility of appropriately analyzing data in a situation where only partial baseline information is available for the potential stocks. Use of an analytical integration approach enhances considerably the numerical performance when the stock mixture structure is challenging (e.g., in the presence of small stocks for which no baseline samples have been collected).

Contrary to the earlier Bayesian methods introduced in Corander et al. (2003, 2004), we have exploited a considerably less computationally intensive strategy that is based on stochastic optimization instead of MCMC simulation. To obtain stable estimates for moderate to large data sets, many long parallel MCMC chains would be needed, but the process for obtaining these chains often is not feasible under a single CPU architecture. Our intelligent search strategy, instead of the random search used in MCMC, seems to resolve this problem very efficiently. A disadvantage of stochastic optimization compared to optimization with MCMC is that a statistically consistent estimate of the number of stocks contributing to the sample cannot be derived. Nevertheless, our novel method has performed satisfactorily in this respect under realistic sampling scenarios. We are currently exploring possibilities for using intelligent proposals in MCMC and an online-based parallel implementation of the method, both of which would provide an ideal framework for biologists using molecular data in stock mixture estimation.

The most relevant biological assumptions used in our approach are HWE and nonlinkage of the marker loci. The latter assumption is generally valid, at least approximately, for the microsatellite markers often used in

Table 4

Allocation of 30 sample individuals from each of five stocks (150 individuals in total) under different baseline settings: (**A**) no baseline, (**B**) 40 baseline individuals from TornW, (**C**) 40 baseline individuals from TornW and Ii, (**D**) 15 baseline individuals from TornW and Ii, (**E**) 15 baseline individuals from Simo. Each "C" refers to an inferred putative stock for which no baseline information was available. Stocks correspond to five different rivers: Tornionjoki (TornW), Simojoki (Simo), Iijoki (Ii), Oulujoki (Oulu), and Neva.

		Allocation				
	Origin	C1	C2	C3	C4	C5
A	TornW	3	1	0	3	23
	Simo	1	1	0	25	3
	Ii	0	1	0	4	25
	Oulu	0	28	0	0	2
	Neva	0	1	29	0	0
		TornW	C2	C3	C4	
B	TornW	28	1	1	0	
	Simo	2	27	1	0	
	Ii	26	4	0	0	
	Oulu	2	0	28	0	
	Neva	0	0	0	30	
		TornW	Ii	C3	C4	C5
C	TornW	22	6	1	1	0
	Simo	1	2	26	1	0
	Ii	5	25	0	0	0
	Oulu	3	1	0	26	0
	Neva	0	0	0	0	30
		TornW	Ii	C3	C4	
D	TornW	24	5	0	1	
	Simo	1	2	0	27	
	Ii	5	23	0	2	
	Oulu	29	1	0	0	
	Neva	0	1	29	0	
		Simo	C2	C3	C4	C5
E	TornW	12	2	1	15	0
	Simo	29	1	0	0	0
	Ii	24	0	0	5	1
	Oulu	1	0	28	1	0
	Neva	0	0	0	0	30

Table 5

(**A**) Average numbers of allocations (over 20 replicates) to the different stocks under an uneven sample size distribution: TornW, n=60, Simo, n=20, Ii, n=30, Oulu, n=5, Neva, n=10. Stocks correspond to five different rivers: Tornionjoki (TornW), Simojoki (Simo), Iijoki (Ii), Oulujoki (Oulu), and Neva. The number of baseline individuals available from each of the five stocks was 30. The column with the heading "Other" refers to additional stocks inferred by the method. The results in (**B**) are otherwise based on an analogous configuration, except that 5% of the marker data was randomly set as missing values.

		Allocation					
	Origin	TornW	Simo	Ii	Oulu	Neva	Other
A	TornW	47.5	1.2	7.9	3.2	0.0	0.3
	Simo	0.6	18.9	0.3	0.2	0.1	0.0
	Ii	3.1	1.2	25.3	0.5	0.0	0.0
	Oulu	0.3	0.0	0.1	4.7	0.0	0.0
	Neva	0.0	0.1	0.1	0.0	9.9	0.0
B	TornW	47.4	1.7	7.2	3.6	0.2	0.2
	Simo	0.6	18.4	0.8	0.3	0.0	0.1
	Ii	3.5	1.1	25.0	0.5	0.0	0.1
	Oulu	0.3	0.1	0.1	4.6	0.0	0.0
	Neva	0.0	0.1	0.0	0.1	9.9	0.1

Table 6

Average conditional posterior probabilities (over 20 replicates) for allocations of individuals to the different stocks under an uneven sample size distribution: TornW, n=60, Simo, n=20, Ii, n=30, Oulu, n=5, Neva, n=10. Stocks correspond to five different rivers: Tornionjoki (TornW), Simojoki (Simo), Iijoki (Ii), Oulujoki (Oulu), and Neva. The number of baseline individuals available from each stock was 30. The column with the heading Other refers to additional stocks inferred by the method.

	Allocation					
Origin	TornW	Simo	Ii	Oulu	Neva	Other
TornW	0.80	0.03	0.13	0.04	0.00	0.00
Simo	0.02	0.94	0.03	0.01	0.00	0.00
Ii	0.12	0.04	0.82	0.03	0.00	0.00
Oulu	0.06	0.01	0.03	0.90	0.00	0.00
Neva	0.00	0.00	0.00	0.01	0.99	0.00

stock mixture analyses. Minor deviations from HWE are not expected to notably affect our inference method; however, presence of samples from small stocks under strong inbreeding could result in an overestimation of k when there is limited baseline information available. Samples from such stocks would tend to be split into parts by the model if no baseline information about the stock allele frequencies can be used to identify the joint origin.

In addition to the molecular markers, auxiliary information, such as simultaneous catch at a common geo-

Table 7

Average numbers of allocations (over 20 replicates) to the different stocks under an uneven sample size distribution: TornW, n=60, Simo, n=20, Ii, n=30, Oulu, n=5, Neva, n=10. Stocks correspond to five different rivers: Tornionjoki (TornW), Simojoki (Simo), Iijoki (Ii), Oulujoki (Oulu), and Neva. The number of baseline individuals available from each of the five stocks was 30. The column with the heading "Other" refers to additional stocks inferred by the method. The marker loci used for inference were randomly sampled from the original nine microsatellites for each replicate; in (**A**) seven loci were used, in (**B**) five loci were used.

		Allocation					
Origin		TornW	Simo	Ii	Oulu	Neva	Other
A	TornW	44.5	3.2	7.6	4.3	0.2	0.0
	Simo	0.9	17.8	0.9	0.4	0.0	0.1
	Ii	2.8	1.6	24.7	0.9	0.1	0.0
	Oulu	0.3	0.1	0.2	4.5	0.0	0.0
	Neva	0.0	0.0	0.0	0.0	10.0	0.0
B	TornW	37.3	4.5	9.3	5.5	0.5	3.1
	Simo	1.0	16.5	1.4	0.6	0.2	0.4
	Ii	3.3	2.8	21.2	2.2	0.1	0.5
	Oulu	0.5	0.2	0.4	4.0	0.0	0.1
	Neva	0.1	0.0	0.1	0.2	9.6	0.2

graphical location, can be incorporated into the analysis. This information is incorporated by the pre-assignment of individuals in the catch data to *a priori* sampling units, when such are considered to be relevant for the species under investigation. Such prior information is particularly useful if the available molecular data are scarce because it enhances the statistical power to detect correct stock origins, as illustrated in our example analyses.

Although the Bayesian method that we propose seems to be a versatile tool for stock mixture identification, certain modifications of the model would also provide fruitful extensions for a variety of biological settings. Current use of the auxiliary information necessitates that the individuals assigned to the same sampling unit represent with certainty the same origin. However, the existence of such conclusive information cannot be assumed in applications in general. There is still a possibility of incorporating information about a tendency to a geographical clustering among the catch individuals with respect to the stock origin, through a suitable modification of the prior distribution of the partitions. In general, use of biological information concerning the behaviour of a species, in combination with geographical sampling information, provides a rich area for further model development. In particular, this combination of information highlights the potential use of the Bayesian statistical framework because the relevant biological information can often be efficiently incorporated through the prior distributions for the model parameters.

Table 8

Allocation of the 25 sample individuals from each of five stocks (125 individuals in total) under different baseline settings: (**A**) no baseline, (**B**) 15 baseline individuals from each stock, (**C**) 15 baseline individuals from each stock, and auxiliary biological information was introduced by considering the simulated catch data as sampling units of the size of five individuals. Stocks correspond to five different rivers: Tornionjoki (TornW), Simojoki (Simo), Iijoki (Ii), Oulujoki (Oulu), and Neva. Each "C" refers to an inferred putative stock for which no baseline information was available.

		Allocation			
Origin		C1	C2	C3	C4
A	TornW	20	0	4	1
	Simo	2	0	2	21
	Ii	20	1	3	1
	Oulu	1	0	24	0
	Neva	0	24	1	0
		TornW	Simo	Ii	Oulu	Neva
B	TornW	18	0	7	0	0
	Simo	2	23	0	0	0
	Ii	0	1	23	1	0
	Oulu	2	0	0	23	0
	Neva	0	0	0	1	24
		TornW	Simo	Ii	Oulu	Neva
C	TornW	25	0	0	0	0
	Simo	0	25	0	0	0
	Ii	0	0	25	0	0
	Oulu	0	0	0	25	0
	Neva	0	0	0	0	25

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The migration patterns of bluefish (*Pomatomus saltatrix*) along the Atlantic coast determined from tag recoveries

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Abstract—Bluefish (*Pomatomus saltatrix*) were tagged and released in Atlantic coastal areas between Massachusetts and Florida from 1963 through 2003 as part of a National Marine Fisheries Service (NMFS) project and a volunteer program sponsored by the American Littoral Society (ALS). A total of 15,699 bluefish were tagged by NMFS and 20,398 by ALS volunteers and 4.3% (1075 NMFS tags and 464 ALS tags) were recaptured and reported. Time-at-large was limited; 65.8% of the recaptured tags were returned within two months of tagging, although nineteen of the returned tags remained at large for two years or more. Tag returns indicated seasonal migrations of fish between the Middle Atlantic Bight and Florida. Three groups of bluefish are proposed for Atlantic coastal waters on the basis of tag return data and are defined by the seasonal occurrence of fish between 30 and 45 cm fork length. The northern group occupied the area from Massachusetts to Delaware between late spring and late fall. Bluefish in the central region between Maryland and North Carolina represented a combination of seasonal transient and resident fish, as did the southern group in Florida. Mixing occurs among all three groups; and larger fish (>45 cm) spend winters in offshore areas. Estimates of von Bertalanffy growth parameters from tagging data were comparable to scale-based estimates. Swimming speeds between point of release and recapture averaged 2.6 km per day, and seasonal spikes greater than 5 km per day corresponded with periods of migration in spring and autumn.

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Bluefish (*Pomatomus saltatrix*) is a pelagic species with a worldwide distribution in temperate and subtropical oceans. In the United States, bluefish are found along the Atlantic coast from southern Florida to Cape Cod, Massachusetts, and occasionally as far north as Nova Scotia (Collette and Klein-MacPhee, 2002). The broad-scale seasonal movements of bluefish are known within the commercial and recreational fishing communities (Hersey, 1987), but details of the migratory pattern remain poorly documented in the scientific literature. Tagging studies provide the most direct evidence of seasonal movements, but the only published account for the Atlantic coast stock is a study in Long Island Sound by Lund and Maltezos (1970). Wilk (1977) provided a description of bluefish migration that remains the accepted standard and which was based on seasonal distribution of commercial and recreational catches, as well as on unpublished results of a tagging project conducted during the 1960s by David Deuel and colleagues at the NMFS James. J. Howard Marine Sciences Laboratory (formerly known as the Sandy Hook Marine Laboratory). The proposed migration involved a north–south coastal movement between New York–New Jersey offshore waters and southeastern Florida offshore waters during the fall and a return spring migration along the same route. Larger fish (i.e. greater than three pounds) were believed to follow a more offshore pathway.

The identification of distinct bluefish stocks contributing to this migratory group has been the subject of multiple investigations. The racial composition of bluefish on the Atlantic coast was investigated by Lund (1961) who concluded, primarily from differences in the number of gill rakers of small bluefish, that six races existed along the coast. Lassiter (1962) found differences in first year growth on scales, which indicated that two groups of fish inhabited North Carolina waters. Returned tags from bluefish tagged in the Long Island area

(Lund and Maltezos, 1970) also indicated two distinct stocks, although not necessarily the same groups as defined by Lassiter (1962). More recently, some scientists have concluded that either two distinct spawning groups exist (Norcross et al., 1974; Kendall and Walford, 1979) or one stock with two distinct survival periods (Hare and Cowen, 1993; Smith et al., 1994). Others, probing mitochondrial DNA (mtDNA) (Graves et al., 1993), have concluded that Atlantic coast bluefish constitute a single population. A discriminant function analysis of morphometric data has corroborated the one stock hypothesis despite evidence of phenotypically plastic characteristics (Austin et al., 1999).

Mark-recapture experiments provide an empirical method for evaluating both migratory behavior and stock composition. In 1962, the National Marine Fisheries Service (NMFS) initiated a study of the migratory patterns of bluefish to obtain information on the population structure of the Atlantic coast stock; this coastwide tagging program continued until 1967. The American Littoral Society (ALS) also coordinates an annual tagging program by private citizens that has resulted in 20 years of tag releases for a variety of species, including bluefish. This combined tag-recapture information constitutes the largest known tagging database for this species. The goal of our study was to investigate the migratory behavior of bluefish along the Atlantic coast by using the results of these previously unpublished tagging studies and to examine the single stock hypothesis in context of tag recovery information.

Materials and methods

The NMFS bluefish tagging program used several types of tags (variously colored). Field tests in 1963 indicated that a dorsal loop spaghetti tag would be more suitable, owing to a longer retention rate, than dart tags or jaw tags. This loop tag, described by Watson (1963), was closed with a pressure-fitted V-shaped clip. In addition, two other types of dorsal loop tags (both closed by knotting the ends of the tubing, and one having a clear outer covering) and an internal anchor tag (5/16 by 1-1/4 inches, with a 3″ streamer as described by Topp [1963]) were used. For visibility of the tags to fishermen, orange was chosen as the color for most of the dorsal loop tags and yellow for the streamer of the internal anchor tags. The fork length of each fish tagged and released was measured to the nearest cm. Recapture information was mailed to NMFS in Sandy Hook, NJ, and included data on recapture location, recapture date, fish length (usually in inches), and weight (lbs and oz, when possible).

The ALS program uses yellow dorsal loop tags that are inserted with a hollow needle through the muscle below the dorsal fins and tied with a simple overhand knot or, as in some recent tags, fastened with a snaplock mechanism (Carlsen, 2000). Details on the date, location of release, fork length (to the nearest inch), and weight (lbs and oz, when possible) were furnished by the fishermen at the time of release. Information regarding tag recapture (including location, recapture date, fish length [inch] and weight) was mailed to ALS headquarters by the fishermen and the distance of the recapture location from shore was coded as inland, inshore (≤3 miles), or offshore (>3 miles). Not all tags recaptured in the ALS program were reported with complete details. As a result, some of the sample sizes presented in the present study differ among analyses, depending on the available data of the recaptured tags. Also, in order to standardize data from both programs and to minimize precision error resulting from unit conversions, fish length data are presented in centimeters followed by the inch equivalent rounded to the nearest whole number.

Several types of fishing gear were used to capture bluefish in the NMFS tagging program. Fish were captured by using gill nets deployed from research vessels, hook and line, commercially operated pound nets, and beach seines; bluefish tagged in the ALS program were captured with hook and line.

Bluefish tagged in the NMFS program were released in areas of seasonal abundance from southeastern Florida to Massachusetts, and major tagging efforts were made in southern Florida, North Carolina, Virginia, New Jersey, and New York (Fig.1). ALS tag releases were concentrated in the New York–New Jersey area, although tagging occurred from Florida to New England (Fig.1). Each ALS recapture location was categorized into 1 of 59 geographic areas and was assigned a latitude and longitude based on the center point of the recapture area. NMFS recaptures were assigned latitude and longitude coordinates based directly on recapture location.

Distance (km) traveled was calculated as the great circle distance between the point of release and point of recapture (NMML[1]) and there was a suitable waypoint if the pathway traversed land. Swimming speed was calculated as the linear distance traveled divided by days at large. In order to allow for acclimation to the presence of the tag, fish recovered within the first three days of release were not included in analyses. Additionally, because speed calculations were influenced by the number of days at large, speed estimates per two-month increments were restricted to tags recovered within 30-day periods to minimize recoveries spanning several months and to avoid averaging speed over various migratory phases. Swimming speeds were compared among months by using an analysis of variance (ANOVA) (Zar, 1974). Comparison of movements by size was made for 5-cm length classes to reduce potential bias from measurement error of recaptured fish.

Bluefish growth was modeled by using the change in fork length during the time-at-large. Von Bertalanffy growth curve parameters L_∞ and K were calculated by using the Fabens model (Fabens, 1965):

[1] NMML (National Marine Mammal Laboratory). 2004. Excel geometry functions. Website: http://nmml.afsc.noaa.gov/Software/ExcelGeoFunctions/excelgeofunc.htm [accessed 4 October 2004].

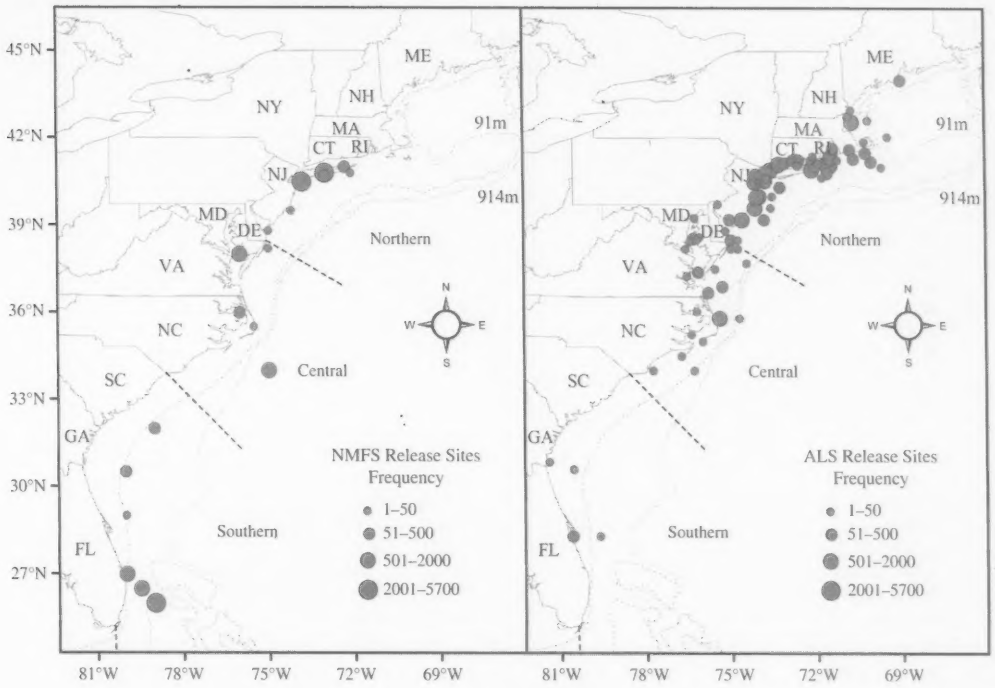

Figure 1

Distribution of release sites (by region) for bluefish (*Pomatomus saltatrix*) released during National Marine Fisheries Service (NMFS) (1963–1967) and American Littoral Society (ALS) (1983–2003) tagging programs.

$$L_{r,i} = L_{t,i} + (L_\infty - L_{t,i})(1 - e^{-K\Delta t_i}),$$

where $L_{r,i}$ = length at time of recapture;
$L_{t,i}$ = length at time of release; and
Δt_i = change in time (years) between release and recapture.

Parameter estimates were derived by using the SAS NONLIN procedure (SAS Inst., Inc., Cary NC). ALS and NMFS data were modeled separately because of a difference in the resolution of size measurements at release (centimeters for NMFS and inches for ALS). Bluefish at large less than 14 days, or fish with zero or negative growth, were excluded from the calculations.

Geographic distributions for tag recoveries were compared with commercial catch locations of bluefish reported from the Middle Atlantic Bight. NMFS vessel logbooks from commercial fishermen in the Northeast region contain information about landings, discards, and the spatial location of catch. Bluefish catch locations from 2001 to 2003 were summarized by month for all gear types. Length samples (measured to the nearest cm) collected by NMFS port agents from commercial landings were expanded to represent length distributions of total reported landings.

Results

During 1963 to 1967, the NMFS bluefish project tagged and released 15,699 bluefish; of these, 11,624 fish (74.0%) were captured with gill nets, 1393 (8.8%) with hook and line, 907 (5.8%) from beach seines, and 1775 (11.3%) from pound nets. Included in the hook-and-line total were 224 fish tagged by volunteer sportsmen in south Florida, New Jersey and New York (which resulted in 17 recaptures). The number of bluefish tagged and released are summarized by month and area in Table 1. From 1983 to 2003, recreational hook-and-line fishermen in the ALS tagging program caught and released 20,398 bluefish. Later recaptures totaled 1539 fish, of which 1075 were NMFS tagged and 464 were ALS tagged.

The NMFS rate of tag return varied by capture method, tag type, and tagging area. The highest return rates (9.6 %) were from pound net releases that could be attributed, in part, to a high recapture rate immediately after tagging. The second highest percentage (6.9 %) and largest number of recaptures (802) were fish captured with gillnets. Although only 4.7% of the fish released from hook-and-line gear were returned, over half of these released fish were from the first year of the tagging program (775 fish tagged, 16 returned, 2.1%),

Table 1

Number of bluefish (*Pomatomus saltatrix*) tags released by month and location of National Marine Fisheries Service (NMFS) and American Littoral Society (ALS) programs.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
NMFS														
North	New England								4	26				30
	New York						196	31	1082	1859	150			3318
	north New Jersey						614	614	2651	1811				5690
	south New Jersey						3	1	4					
Central	Maryland						20							20
	Virginia					964	4							968
	North Carolina					127	274	40	57	43	569			1110
South	South Carolina				60	19								79
	north Florida				335	335								
	south Florida	510	572	1199	1008						100	425	331	4145
	Total	510	572	1199	1403	1110	1111	686	3794	3739	819	425	331	15,699
ALS														
North	New England	1	1		3	124	846	1233	1470	1845	1410	440	1	7374
	New York				3	368	803	568	568	661	1143	323	2	4439
	north New Jersey				76	1383	1181	814	956	961	837	411	22	6641
	south New Jersey					4	90	18	18	25	26	11		192
Central	Maryland					35	66	21	35	32	63	5	2	259
	Virginia				8	153	122	8	6	3	5	18	14	337
	North Carolina				11	21	6	4	14	10	421	124	26	637
South	South Carolina													
	Georgia				7	2		1	3	2	2	1		18
	Florida	122	43	59	93	24	1	5	2	9	23	20	100	501
	Total	123	44	59	201	2114	3115	2672	3072	3548	3930	1353	167	20,398

whereas the remainder of the hook-and-line releases (618 fish) resulted in 49 recaptured fish (7.9%). This difference may be attributable to less effective tags used during 1963, rather than the capture method. All ALS releases were fish caught with hook and line, but gear type was not recorded for the recaptured fish.

Tag types differed in rates of return and in time fish spent at large. Return rates for NMFS tags were similar between dorsal loop tags (760 of 10,752; 7.1%) and internal anchor tags (310 of 4441; 7.0%). All NMFS tagged fish recaptured after 17 months at liberty had been tagged with internal anchor tags. Abrasion of some dorsal tags occurred after two months and appeared more severe on tags returned from Florida releases. Some abrasion occurred on the external streamer of the internal anchor tags. ALS dorsal loop tags resulted in an overall return rate of 2.2%.

Return rates for the NMFS tags varied by area, from 4.5% in New York to 10.2% from Florida (Table 2). Eighty-three percent of recaptured tags that were at liberty one year (n=24) were from tagging in areas north of New Jersey, and all recaptured tags at liberty 2, 3, and 4 years (10, 4, and 4 fish recaptured, respectively) were also from tagging in these areas (Table 2). For all areas combined, 51.3% of the NMFS recaptured fish were at liberty less than one month and 88.1% were at liberty less than five months. Among ALS tags, 50.3% were at liberty for two months and 79.3% for five months or less. Only 4.5% of all returned fish were at liberty greater than one year and 1.2% greater than two years. The longest time-at-large for an ALS tagged bluefish was 1461 days and 1486 days for a NMFS-tagged fish.

The size at release of the 36,097 tagged bluefish differed between the two programs. Fork lengths (FL) ranged from 19 to 57 cm (7 to 22 inch) for NMFS and 15 to 114 cm (6 to 45 inch) for ALS (Fig. 2). The majority of fish released in the NMFS program (83.1%) were 30 to 45 cm (12 to 18 inch) and were 1-, 2-, or 3-year-olds according to estimates determined from scales from a subsample of similar size fish collected during the tagging operations. A greater size range of bluefish were tagged in the ALS program, and 88.2% measured 30 to 76 cm (12 to 30 inch).

Size frequencies of bluefish released, and of those subsequently recaptured, differed despite the relatively short times at large (Fig. 2). Changes in length can be attributed to growth, unit conversion, and associated measurement error. The NMFS recapture data set had 616 tag recoveries with appropriate fork length and time-at-large information, whereas the ALS set had 336 with these data (Fig. 3). The von Bertalanfy growth parameter estimates from these data were L_∞ of 100 cm and 118 cm (39 and 46 inch) for NMFS and

Table 2

Number of bluefish (*Pomatomus saltatrix*) tags returned from each release area by months at liberty. ALS = American Littoral Society; NMFS = National Marine Fisheries Service; NE = New England; NY = New York; NJ = New Jersey; MD = Maryland; VA = Virginia; NC = North Carolina; SC = South Carolina; FL = Florida.

	ALS							NMFS									
Month	NE	NY	NJ	MD	VA	NC	FL	NE	NY	NJ	VA	NC	SC	FL	ALS total	NMFS total	Combined total
0	20	48	40	3	3	2	9	1	36	178	34	37	2	265	125	552	677
1	32	30	38		1	2	3		30	68	9	17	2	102	106	229	335
2	20	27	24		4		3		5	32	7	6	1	43	78	94	172
3	7	15	14				3		7	10	4	4		22	39	47	86
4	5	5	6						3	4	6	2		10	16	25	41
5	3	3	1							4	3	3		4	7	14	21
6	2	1	1						4	1		1		3	4	9	13
7	3	7	1		1					1	2				12	3	15
8	4	12	2						3	3		1		1	18	8	26
9	1	6							8	3				1	7	12	19
10	4	5	4						13	4		1			13	18	31
11	1	5	2						12	6	1			2	8	21	29
12	1	5	3		1				6			1		1	10	8	18
13	2	3							6	3				1	5	10	15
14	1		1						1	2					2	3	5
15		1													1	0	1
16		1									1				1	1	2
17											1				0	1	1
18															0	0	0
19														1	0	1	1
20									1						0	1	1
21															0	0	0
22	2								1						2	1	3
23	1								3						0	3	3
24									3						1	3	4
25+	3	1						1	7	3					4	11	15
No. recaptured	112	175	137	3	10	4	18	2	149	322	68	73	5	456	459	1075	1534
No. released	7374	4439	6833	259	337	637	519	30	3318	5694	968	1110	79	4480	20,398	15,699	36,097
Return rate	2%	4%	2%	1%	3%	1%	3%	7%	4%	6%	7%	7%	6%	10%	2%	7%	4%

ALS, respectively, and K values of 0.230 and 0.206, respectively. The 95% confidence interval around L_∞ for the NMFS data ranged from 79 to 121 cm (31 to 48 inch) and ALS estimates ranged from 95 to 141 cm (37 to 56 inch). Confidence intervals for the K parameter ranged from 0.135 to 0.324 for the NMFS data and 0.109 to 0.303 for the ALS data.

A single vector drawn between tag release and recapture locations represents the shortest possible water route traveled between the two points. The actual route of travel likely diverts from this path; however it remains the basis for determining distance traveled. Movement of bluefish between western Long Island Sound and lower New York Bay through the East River was not indicated by the tag return data, and therefore passage of bluefish through the East River was not considered in the distance calculations. Seventy-five percent of the NMFS tags were recaptured within 100 km of the tagging location; whereas 9.7% were caught 350 km or farther from the tagging area. The maximum distance traveled was 2227 km (Chesapeake Bay to west Florida) for a fish at liberty 341 days (6.5 km per day). For the ALS recaptured fish, 59.7% were recaptured within 100 km of the point of release and 40.3% (187) traveled beyond 100 km averaging 295 km, and 45 bluefish traveled more than 400 km. The maximum distance was 1096 km for a fish at liberty for 76 days (14.4 km/day).

The number of days at liberty represents the maximum time possible for a fish to travel the straight-line distance between the tagging and recapture locations. Movement was generally less than 5 km per day (84.3% of recaptures) and the overall average speed of fish recaptured in both programs was 2.6 km per day. Seventeen bluefish traveled more than 20 km per day and had a maximum swimming speed of 48.3 km per day for three days.

The average swimming speeds for combined NMFS and ALS recaptured fish were significantly different among months (P=0.02). Speeds were highest during the autumn, peaking during October–November at 5.3 km per day, and there was another spike during April–May at 4.9 km per day (Fig. 4). These seasonal peaks were in contrast to the overall average of 2.6 km per day. Seasonal variations in swimming speed were considered indicative of periods of active migratory behavior. This annual cycle of movement was divided into four periods based on the average rate of travel for each month: winter residency (December to February), spring migration (March to May), summer residency (June to August), and autumn migration (September to November).

The swimming speed and distance traveled during seasonal movements were different for all bluefish size groups. Swimming speed of fish 30–45 cm (12–18 inch) was greater than speed of fish 45–65 cm (18–26 inch) and this pattern was consistent across regions (Fig. 5). The speed disparity by size was influenced by the distance traveled, not by differences in time-at-large because the data were limited to recoveries within 90 days. Smaller bluefish, particularly those released in the northern region, traveled farther distances on average than fish in the larger size classes (Fig. 5).

Movement of tagged fish among areas is a function of both the behavior of the animal and adequate time-at-large to exercise that behavior. Half (229 of 459 fish with location information) of bluefish tagged with ALS tags were recaptured beyond the state of release; the remaining recaptured fish were caught in the area of release (Table 3). NMFS releases had a higher proportion recaptured bluefish within the state of release (77.1%; Table 3). Most long distance returns occurred during the first year after tagging; recoveries in years 1 through 4 after tagging were generally from the area of release (62 of 100) or in the release area and adjacent areas (91 of 100). Fish recaptured from New Jersey northward accounted for 89 of the 100 recaptured

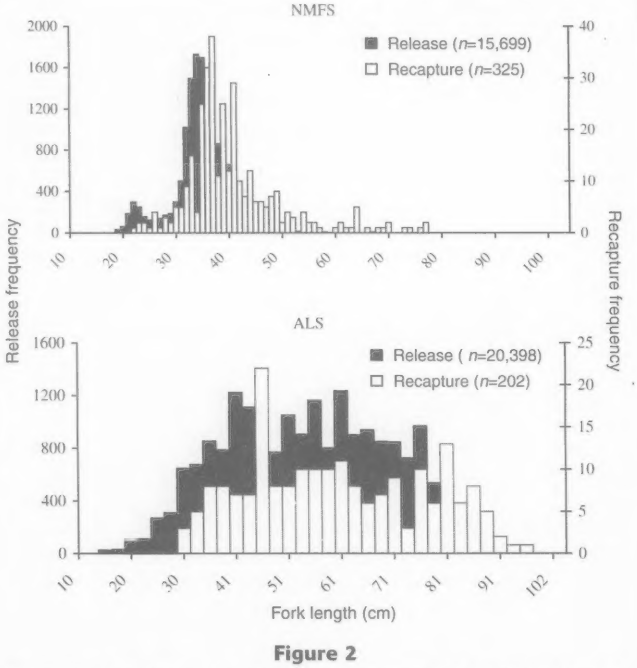

Figure 2

Frequency distributions for release and recapture fork lengths of bluefish (*Pomatomus saltatrix*) sampled in National Marine Fisheries Service (NMFS) and American Littoral Society (ALS) tagging programs.

fish after one year at liberty, and all but two of these were from releases in this area. The higher percentage of recaptured fish from Florida may reflect greater annual fishing effort in contrast to northern areas.

Seasonal recaptures of tagged bluefish along the coast (Fig. 6) were a function of both fishing effort and the abundance of tagged fish in the area. Over ninety-one percent of all recaptured NMFS fish (978 of 1,075) were caught in inshore areas (including Chesapeake Bay, Delaware Bay, and Long Island Sound) or within one mile of the coast. Of the remaining 99 recaptures: one fish was caught 75 miles offshore and the rest within 30 miles of the coast; 47 between 1 and 6 miles, 40 between 6 and 20 miles, and 9 between 20 and 30 miles. Tagged fish released in New York and New Jersey accounted for 45 of the 50 returns over 6 miles offshore; 4 of those remaining fish were both released and recaptured off Florida, and the last fish had been released in Florida and recaptured off New Jersey. All of these 45 returns released from New York and New Jersey were recovered north of Delaware—most off New Jersey and New York. The offshore returns occurred from May through November, although most of the fall recaptured fish had been released during the same season (21 of the 23 recaptures in September, October, and November), whereas most spring and summer recaptured fish had been at liberty for at least one year (19 of the 22 recaptures from May though July).

Seasonal patterns of bluefish migration, determined from information within recovered tags, generally followed one of three patterns: north–south between the northern Middle-Atlantic and Florida; a north–south pattern within the Middle-Atlantic; and year round movements between inshore and offshore Florida. To simplify examination of migration patterns, recapture locations were divided into three regions. The area from Delaware to New England was designated the northern region, Maryland through North Carolina as the central region, and the area between South Carolina and southern Florida as the southern region. The single fish recovered in western Florida was ignored for our analysis. A recovery matrix by region showed that greater than 90% of the bluefish recaptured within the northern or southern region had originated within the same region (Table 4). However, within the central region, the percentage of recaptured fish originating in that region was only 80.3%. The remaining tags were either recaptured to the north (12.7%) or the south (7.0%). Distribution maps

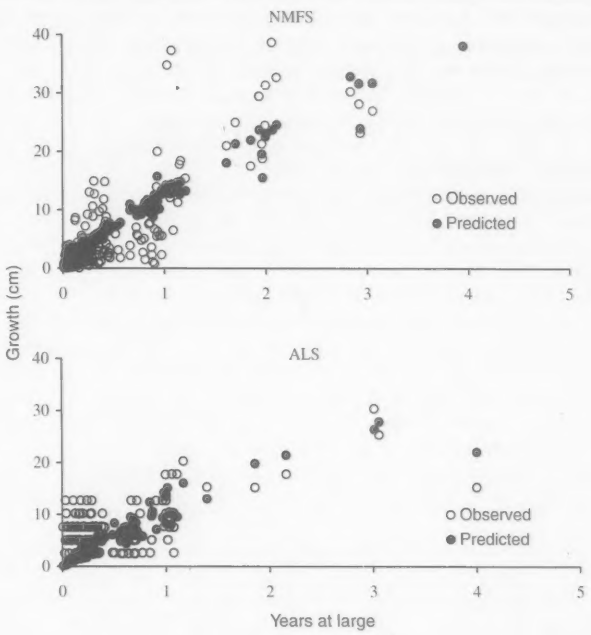

Figure 3

Changes (observed and predicted) in fork length during time at large (years) for bluefish (*Pomatomus saltatrix*) sampled in National Marine Fisheries Service (NMFS) and American Littoral Society (ALS) tagging programs.

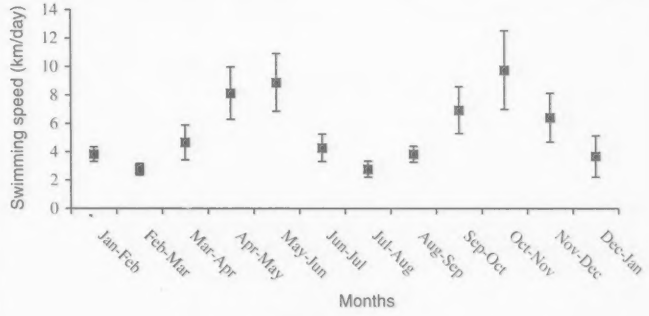

Figure 4

Mean monthly swimming speeds (km/day) of bluefish (*Pomatomus saltatrix*) ±95% confidence intervals from two combined program tag recoveries: National Marine Fisheries Service (1963–1967) and American Littoral Society (1983–2003).

of seasonal recaptured fish (Fig. 6) further highlighted the pattern of a northerly migration that began in May and was followed by southerly migration beginning in December. However, the entire coastal stock did not make the seasonal shift. Bluefish released in southern Florida were recaptured locally during the summer residency period and other fish tagged in southern Florida appeared in coastal New Jersey (Table 3).

Seasonal distribution data from bluefish tag returns indicated a southward movement of fish during the fall, culminating in an over-wintering aggregation near Cape Hatteras, North Carolina, and to the south. Commercial catch records from the Middle Atlantic for 2001 to 2003 indicated a greater seasonal inshore-offshore movement than that implied from tag recoveries. Vessel logbook data indicated that bluefish are present in the northern and central areas throughout the winter and have an increasingly offshore and southern distribution as water temperatures decrease. By March, the commercial catches increase off the coasts of Virginia and North Carolina (Fig. 7). The sizes of fish in these commercial catches were generally larger than those of tagged fish; lengths were between 25 and 70 cm and mean size was 45 cm. The commercial catch distribution expanded northward beginning in April, in a direction similar to the bluefish migratory route indicated by spring tag returns.

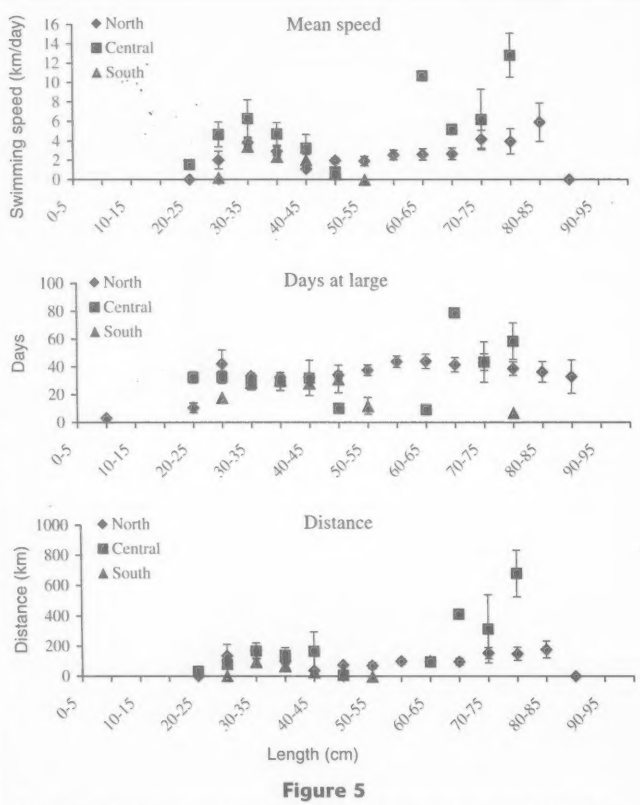

Figure 5

Mean swimming speed, days at large, and distance traveled (±95% confidence interval) by length for bluefish (*Pomatomus saltatrix*) sampled in National Marine Fisheries Service and American Littoral Society tagging programs.

Discussion

A generally established hypothesis for bluefish migration is that fish undergo a seasonal coastal migration, leaving the Mid-Atlantic Bight in autumn as water temperatures decrease and moving as far south as Florida. In spring, bluefish return north where they spend the warmer months in habitat suitable for larger, mature fish—possibly in habitat extending across the continental shelf (Wilk, 1977; Fahay et al., 1999). Our hypothesis expands that migration pattern to suggest there are three bodies of fish with different migration behaviors. One group has an extensive north–south migration between New England and Florida, a second group has a migration route within the Mid-Atlantic Bight bounded to the south by North Carolina, and a third group has an inshore-offshore migration within Florida waters. The geographic ranges of these three groups overlap during at least part of the year and the seasonal areas of distributions change with fish size.

Bluefish from Massachusetts to Delaware (northern region) leave the coastal areas in autumn, and fish less than approximately 45 cm (18 inch) migrate south along the coast and are found in the south Florida winter fishery. However, tag return data indicate that part of this size group, as well as all fish over 45 cm (18 inch), move offshore in autumn and are distributed during winter in offshore areas south of Virginia. Both size groups return to the northern area in spring and summer a year after tagging, as well as in successive years.

The Mid-Atlantic area from Maryland to North Carolina (central region) appears to be a transitional area in the migratory route. A group of fish tagged in the northern region migrated in fall to the central region and remained throughout the winter, whereas other fish continued south to Florida. In the spring, a portion of the Florida fish moved back to the central region, while others continued through to the northern region. The distribution of commercial catches reported in logbooks confirmed the movement of bluefish into offshore waters during autumn, and movement increasingly south as winter progresses. The reported landings of large

Table 3

Recapture matrix by state of release for National Marine Fisheries Service (NMFS) and American Littoral Society (ALS) bluefish (*Pomatomus saltatrix*) tag recoveries. NE = New England; NY = New York; NJ = New Jersey; DE/ME = Maine; MD = Maryland; VA = Virginia; NC = North Carolina; SC = South Carolina; FL = Florida.

NMFS	Recapture area										
Release area	NE	NY	north NJ	south NJ	DE/MD	VA	NC	SC	north FL	south FL	west FL
New England		2									
NY	2	96	33	4	1		3		3	7	
north NJ	2	25	210	31	8	2	32		6	6	
south NJ											
DE/MD											
VA			4	1	1	53	5	1		2	1
NC		2	3	1	4	56			5	2	
SC		1	4								
north FL									37		
south FL			3	2	1				36	377	

ALS	Recapture area										
Release area	ME	MA	RI	CT	NY	NJ	DE	MD	VA	NC	FL
AL											
ME		1									
MA		12	3	5		9	1	2	1	3	
RI		8	20	22	16	5		1		4	
CT		5	2	20	18	1	1			1	
NY		7	2	16	82	17	3			3	
NJ		3	3	13	25	65	10	4	2	5	
DE					1		4		1	1	
MD								3			
VA	1	1	1	2	1	2		1		1	
NC										4	
FL											19

bluefish fish during the Virginia–North Carolina winter fishery and the paucity of bluefish over 45 cm (18 inch) in the Florida fishery indicate that the larger fish do not continue the southern migration beyond North Carolina.

Bluefish are found throughout the summer in southern Florida (southern region) as evidenced by tag returns and fishery landings, although at a low level of abundance compared with fall through spring landings. The one fall recaptured tag in New Jersey from a fish released in Florida in the spring (at liberty 17 months) indicates that fish from the southern group are found in northern areas in subsequent years. Bluefish found off Georgia and South Carolina appear to be transitory, and are present primarily in spring and fall. The relative lack of tag recoveries in coastal South Carolina and Georgia implies a migratory pathway farther offshore, possibly closer to the shelf edge and Gulf Stream.

Change in fish size leads to a change in the seasonal migration route. The migratory groups are best defined

Table 4

Tag recovery matrix by region for combined National Marine Fisheries Service and American Littoral Society tags; data correspond to tag release and recaptures shown in Figure 6.

	Recapture region			
Release region	North	Central	South	Recaptures
North	812 (90%)	67 (7%)	22 (2%)	901
Central	20 (12%)	127 (80%)	11 (6%)	158
South	7 (1%)	4 (1%)	469 (98%)	480
Recaptures	839	198	502	1539

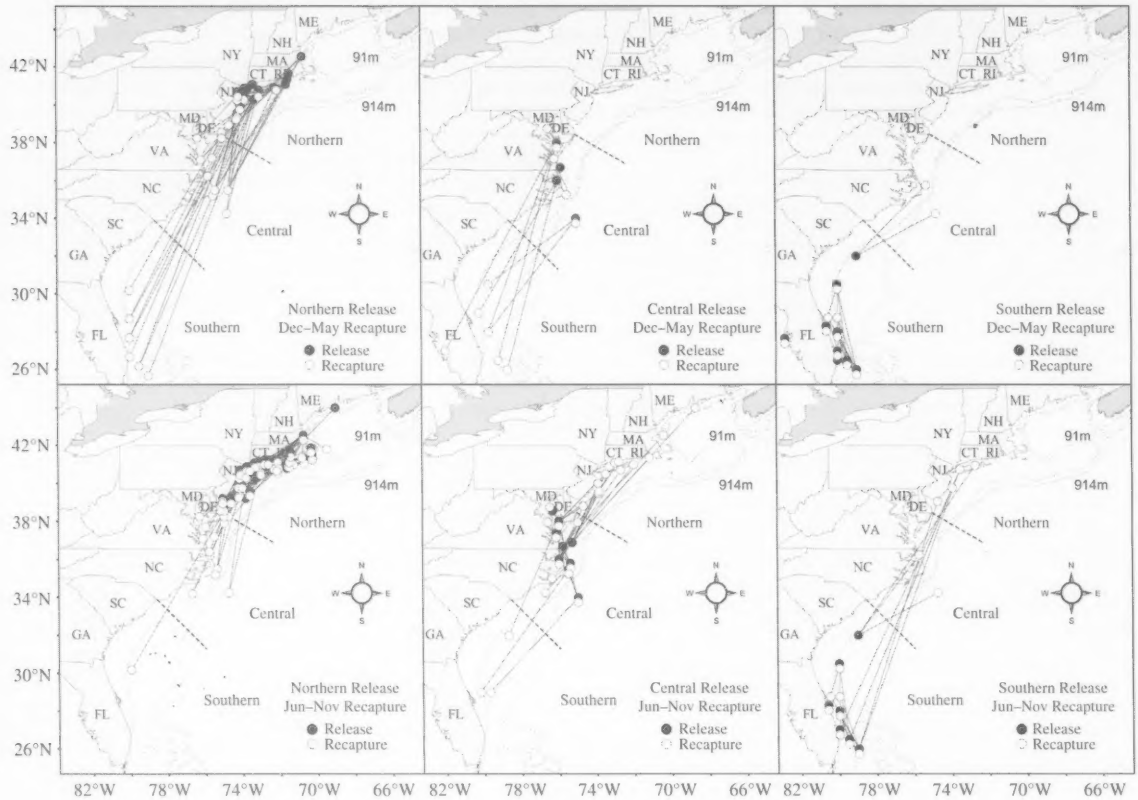

Figure 6

Geographic distribution of tag recoveries, by region of release and season of recapture, for bluefish (*Pomatomus saltatrix*) sampled in National Marine Fisheries Service (NMFS) and American Littoral Society (ALS) tagging programs combined.

by the seasonal aggregations of smaller fish (less than approximately 45 cm, 18 inch FL). Juvenile bluefish use a coastal migratory route that extends farther south and offshore with increasing size. Some fish past the juvenile stage may remain in Florida for a season while others return to northern areas in the first or second spring. As growth continues, north–south migration routes become truncated—replaced by a route that keeps fish within the Mid-Atlantic Bight circuit.

Because migration patterns appear to be size related, growth rate will determine how long individuals maintain a particular migration behavior. Tag-based growth rate estimates (K=0.23 and 0.21) are similar to values reported from scale-based age studies, but the tag model resulted in larger theoretical maximum sizes of 100 and 118 cm (39 to 46 inch). Salerno et al. (2001) reported an average L_∞ value of 87 cm and K equal to 0.26, whereas previously published estimates range from 67 to 128 cm (Lassiter, 1962; Wilk, 1977) and have K values ranging from 0.10 to 0.34 (Lassiter, 1962; Wilk 1977). The tag-based estimates of maximum size are similar in size to that of the largest fish reported in recreational landings (Salerno et al., 2001) and size of this largest fish caught in recreational landings could be considered an empirical estimate of L_∞. Otoliths have been shown to be preferable to scales for aging bluefish (Sipe and Chittenden, 2002). Growth parameters of bluefish from the South Atlantic, aged from otoliths (L_∞=101.9 cm, K=0.10 [Barger, 1990]), compare well with our tag-based estimates of L_∞ but produce very different growth-rate estimates.

The migration route bluefish follow from coastal New England to southern Florida, a distance of potentially >2000 km, is completed over the course of several months. Bluefish held in aquaria have been shown to travel at speeds from 40 to 60 cm/s and to have burst speeds up to 80–110 cm/s (Olla et al., 1970). An approximate average speed for bluefish similar in size to those tagged in the present study would be between 39 km per day (40 cm/s) and 59 km/day (60 cm/s). The majority of tagged fish moved between 0 and 5 km per day (84%), and most (97%) bluefish swam less than 20 km/day. However, several individuals averaged between 55 and 111 km per day. An average swimming speed

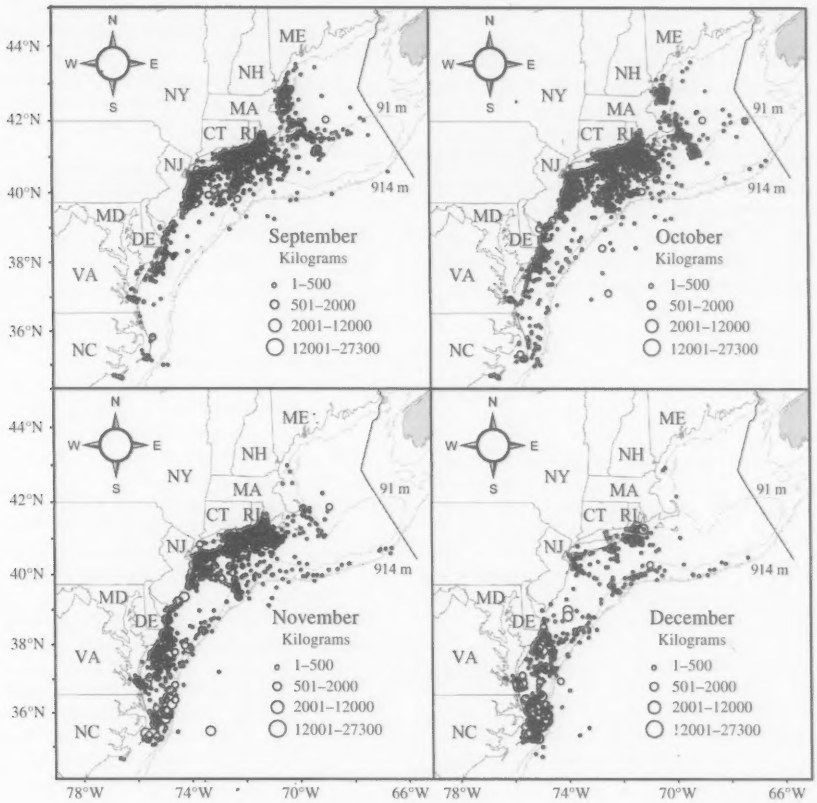

Figure 7

Distribution of bluefish (*Pomatomus saltatrix*) in the Middle Atlantic Bight based on commercial logbook catch records (2001–2003) for all gear types.

greater than 50 km per day would imply that some type of passive transport supplemented active swimming movement. The offshore distribution of bluefish in the South Atlantic Bight during winter, as inferred from tags, may provide an opportunity for bluefish to use the Gulf Stream during the northern migration.

Several recent studies have evaluated the stock structure of bluefish along the Atlantic coast by using genetic material (Chiarella and Conover, 1990; Graves et al., 1993; Davidson, 2002) and morphometric characteristics (Austin et al., 1999). These studies have concluded that bluefish along the U.S. Atlantic coast comprise a single stock. The tag recovery information for bluefish illustrates differences in movement patterns among areas, but these groupings do not imply unique stock characteristics. Consequently, there is no evidence from the tag recovery information that refutes the single stock hypothesis.

Implementation of a well-designed tag and release program is critical for analytical evaluation of migration (Schwarz et al., 1993). Limitations associated with tag recovery must be accounted for in the design of an effective tagging program. Recovery of most tags is a function of fishing effort; therefore recaptured tags must be considered in the context of the fisheries that will provide the recoveries. Unknown variations in fisheries over the past four decades may have influenced the patterns of bluefish tag recoveries in the NMFS and ALS programs, ultimately influencing interpretation of the results. In addition, time-at-large for fish in both programs was generally less than one year which may be due to tag-induced mortality and tag loss (Henderson-Arzapalo et al., 1999). Bluefish tagged in Western Australia were generally at large for less than a year and experienced tag losses between 25% and 38% (Young et al., 1999). The NMFS and ALS programs demonstrate that tagging is a viable tool in analyses of bluefish populations, but it has limitations. Using the knowledge gained from these tagging programs, scientist may find that a renewed tagging effort incorporating recent technological advances will provide further insight into the migratory behavior of bluefish and, in particular, the behavior linked to environmental cues.

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Evaluating light-based geolocation for estimating demersal fish movements in high latitudes

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Abstract—We evaluated light-based geolocation estimates from pop-up satellite tags in high latitudes because some of the largest fisheries in the world are in areas where this technique has not been assessed. Daily longitude and latitude were estimated by using two Wildlife Computers software programs: 1) Argos Message Processor (AMP), which summarizes light intensity data transmitted to satellites, and 2) Time Series Processor (TSP), which uses more detailed data obtained from retrieved tags. Three experiments were conducted in the northern Gulf of Alaska using tags placed on 1) Pacific halibut in outdoor aquaria, 2) a fixed mooring line at various depths and 3) wild Pacific halibut. TSP performed better than AMP because the percentage of days with geolocation estimates was greater and the mean error magnitude and bias were smaller for TSP and increased with depth for both programs; however, latitude errors were much greater than longitude errors at all depths. Light-based geolocation enabled us to discern basin-scale movements and showed that the Pacific halibut in our study remained within the Gulf of Alaska. We conclude that this technique provides a feasible method for inferring large-scale population structure for demersal fishes in high latitudes.

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Demersal fishes at high latitudes support some of the most lucrative fisheries in the world. An example is the Pacific halibut (*Hippoglossus stenolepis*) fishery off Canada and the United States. Currently, the International Pacific Halibut Commission (IPHC) manages the Pacific halibut population as a single, panmictic stock from northern California through the eastern Bering Sea based on genetic (Grant et al., 1984; Bentzen et al., 1998) and tagging data (Skud, 1977). However, Pacific halibut movements and population structure are not fully understood and mixing may be more restricted than assumed, as evidenced by a number of local depletions in recent years (Hare[1]). A method for estimating movements over large distances is needed to improve the ability to identify populations and manage the harvest. Population structure and movement information is needed for management of several other high-latitude fisheries including Atlantic halibut (*Hippoglossus hippoglossus*), Pacific cod (*Gadus macrocephalus*) and Greenland turbot (*Reinhardtius hippoglossoides*) (Godø and Haug, 1988; Shimada and Kimura, 1994; Albert, 2002).

New methods using information collected by electronic tags, which contain miniaturized onboard computers, are providing location estimates of demersal marine fishes (see review in Arnold and Dewar, 2001). One such method, the tidal location method, has been used to geolocate North Sea plaice (*Pleuronectes platessa*) (Hunter et al., 2003). This method compares the tidal range and time of high

[1] Hare, S. R. 2005. Investigation of the role of fishing in the Area 4C CPUE decline. Int. Pac. Halibut Comm. Report of Assessment and Research Activities 2004:185–198. Int. Pac. Halibut. Comm, PO Box 95009, Seattle, WA 98145-2009.

water, as measured by the depth sensor of the electronic tag, to those predicted by tide models. Unfortunately, we are unable to use this method near Alaska because the water depth is much greater than in the North Sea. Deep water necessitates that the depth sensor of a tag have a greater range, which decreases depth resolution. Thus, tags used off Alaska have a depth resolution that is greater than the tidal range; therefore the tag cannot distinguish tidal fluctuations.

Another tagging method has been used to geolocate Baltic Sea cod (*Gadus morhua*) (Neuenfeldt et al.[2]). This method is based on combined data of depth, temperature, and salinity obtained by electronic tags attached to cod. Hydrographic fields obtained from hydrodynamic modeling are used as a geolocation database to identify daily locations of fish by comparison with the environmental data collected by each electronic tag. Unfortunately, the tags that we used are not available with a salinity sensor and hydrodynamic models of the area are not accurate on the bottom (Hedstrom[3]).

Ambient light data collected by electronic tags may be used to calculate daily estimates of latitude and longitude of fish. Geolocation by light has been implemented successfully on a variety of pelagic species to discern their daily position and movement patterns (Gunn and Block, 2001; Schaefer and Fuller, 2002; Itoh et al., 2003; Sibert et al., 2003).

However, no studies have been conducted to evaluate light-based geolocation estimates from tags attached to demersal fish, nor from fish inhabiting high latitudes. Unfortunately, light levels in deep and high-latitude waters may be low and if the water is turbid, the light may be attenuated very quickly, thus hindering position estimates. Additionally, many demersal fishes inhabit a depth range where geolocation by light has not been evaluated at any latitude.

The goal of this study was to examine the feasibility of using ambient light geolocation for estimating demersal fish movements in high latitudes. This was accomplished by the following procedures: 1) by comparing daily latitude and longitude estimates from two proprietary software types developed by Wildlife Computers, 2) by examining latitude and longitude estimates as a function of depth, and 3) by examining *in situ* latitude and longitude estimates of pop-up archival transmitting (PAT) tags attached to wild Pacific halibut.

Materials and methods

The pop-up archival transmitting tag (PAT, Wildlife Computers, Redmond, WA, vers. 2.0) is a miniature computer that is attached externally to a fish. The tag contains a clock and sensors that collect depth, temperature, and ambient light intensity data at user-specified intervals (Sibert, 2001). On a programmed date, the PAT tag disengages from the fish, floats to the surface, and transmits summaries of the recorded temperature, depth, and light data to Argos satellites; the data are then retrieved by the investigator. If the tag is retrieved, the complete archival record of temperature, depth, and ambient light data may be obtained.

From October 2000 to March 2002, a pilot study was conducted to assess the feasibility of using PAT tags as a tool for identifying critical habitat of demersal fishes in high latitudes (Seitz et al., 2002, 2003). Geoposition estimates were made from light data collected in three experiments in which PAT tags were attached to 1) Pacific halibut in outside aquaria, 2) a stationary mooring, and 3) wild Pacific halibut *in situ*. The temperature and depth data from the wild Pacific halibut experiment and their Argos-based final locations have been reported previously (Seitz et al., 2003).

In the first experiment, two Pacific halibut were captured, transported live to outside aquaria at the Alaska SeaLife Center (Seward, Alaska; 60.099°N, 149.440°W) and tagged on 18 Oct. 2000 with PAT tags programmed to record light intensity every minute. The tags were retrieved on 1 May 2001, and the longitudes and latitudes of Pacific halibut estimated from the tag data were compared with the known location of the Pacific halibut in the aquaria.

A second experiment was conducted by using a fixed mooring to examine latitude and longitude estimates as a function of depth. From December 2000 to April 2002, four PAT tags were attached to a stationary mooring line (the NOAA Alaska Observing System's "GAK-1" mooring) in Resurrection Bay, Alaska (59.852°N, 149.330°W) at depths of 27, 57, 96 and 146 m. These tags were attached to four different current vanes on the mooring line so that their light sensors faced up.

In a third experiment, to evaluate the performance of the light sensor and geolocation algorithm *in situ*, fourteen wild Pacific halibut (108–165 cm fork length) were captured, tagged, and released in November 2000, March 2001, and July 2001 from a commercial longlining vessel in Resurrection Bay, AK, and off Cape Aialik, AK (for details, see Seitz et al., 2002, 2003). Light data were recovered from eight tags. PAT tags were tethered externally to each study animal by a piece of monofilament fishing line secured to a titanium dart that was inserted into the dorsal musculature of the fish. At a user-specified date and time, the PAT tag corroded the pin to which the tether was attached, thus releasing the tag from the animal. The tag floated to the surface and transmitted summarized data records through the Argos satellite system.[4] After the tag popped-up to the

[2] Neuenfeldt, S., H.-H. Hinrichsen, and A. Nielsen. 2004. A method to geolocate eastern Baltic cod by using Data Storage Tags (DSTs), 14 p. Int. Coun. Explor. Sea CM/L:06. Int. Coun. Explor. Sea, H.C. Andersens Boulevard 44-46, DK-1553, Copenhagen V, Denmark.

[3] Hedstrom, K. 2005. Personal commun. Artic Region Supercomputing Center, Univ. Alaska Fairbanks, PO Box 756020, Fairbanks, AK 99775.

[4] Service Argos, Inc. (http://www.argosinc.com). [Accessed on: 13 December 2005.]

surface, its location was determined by the Doppler shift in the transmitted radio frequency in successive uplinks (Keating, 1995). The endpoint position was the first location class (LC) estimate reported in the LC1-3 range, which all have error estimates <1.0 km.

The basis of light-based geolocation is the estimation of times of sunrise and sunset. Two proprietary programs developed by the Wildlife Computers, Argos Message Processor (AMP, vers. 1.01.0007) and Time Series Processor (TSP, vers. 1.01.0008), were used to extract times of sunrise and sunset from light intensity data. AMP identified daily sunrise and sunset times from light data transmitted through Argos satellites or directly from complete archival light records. TSP could be used only to identify sunrise and sunset times from complete archival light data from PAT tags that were physically recovered.

In the next phase, another Wildlife Computers program, Global Position Estimator (GPE, vers. 1.01.0005), used the sunrise and sunset times to calculate the daily longitude and latitude of tags. First, we rejected days with light level curves that did not exhibit smoothly sloping light levels from high to low or low to high (Fig. 1). GPE was used to calculate longitude for the remaining data based on the local noon time of the tag (mean of the sunrise and sunset times). Estimated longitude values that were not possible for a fish released in the Gulf of Alaska were rejected from the data set. For example, an impossible longitude was one that placed the tag on land or outside the published range of the Pacific halibut (i.e., to the west of Hokkaido, Japan (140°E) or to the east of Santa Barbara, CA (117°W; Mecklenberg et al., 2002)). Once longitude was estimated, latitude was estimated by GPE, which used the "dawn and dusk symmetry method" (Hill and Braun, 2001; Musyl et al., 2001). Daily latitude estimates were the theoretical location of expected light levels that best matched the observed light levels measured by the tag. Latitude outliers were removed in the same manner as that used for longitude outliers. For all three experiments, the number of days with geolocation estimates was defined as the days that produced latitude and longitude estimates, after "bad" light curves (Fig. 1) and outliers were removed.

For the tags with known positions in the tank and mooring experiments, we calculated bias and error magnitude based on true locations. Daily positional bias was calculated as the true position minus the estimated position (signed distance between positions), and daily error magnitude was the absolute value of the bias (distance between points). For the tank experiment, we pooled the data from the two tags. Mean error magnitudes of software types were compared by using a two-tailed t-test. For the fixed mooring experiment, we calculated mean positional bias and mean error magnitudes for each tag and software combination. Mean biases were compared to a hypothetical bias of zero by using a two-way (tag and software) ANOVA model (vers. 8, proc GLM, SAS, Cary, NC). Mean error magnitudes were compared by using an ANOVA with a Tukey-Kramer test (Kramer, 1956; vers. 8 proc GLM). For both bias and error magnitude, the means are a measure of accuracy and the standard deviations are a measure of precision.

For wild fish, it was impossible to know the true daily position of each fish for the duration of the experiment. However, for three of the eight tags released on wild fish, geolocation estimates were produced in the first or last six days of deployment. Therefore, we compared the estimated positions of the tags for the six days immediately following release of the tags and for the six days before recapture of the tags or before tags transmitted data to Argos satellites. All three of these tags were physically recovered and TSP produced estimates for all tags. AMP produced plausible estimates for one tag only because other estimates were rejected as outliers. For each comparison, we calculated the mean bias and mean error magnitude, assuming that the fish was stationary (or nearly so) during the first and last six days of the deployment.

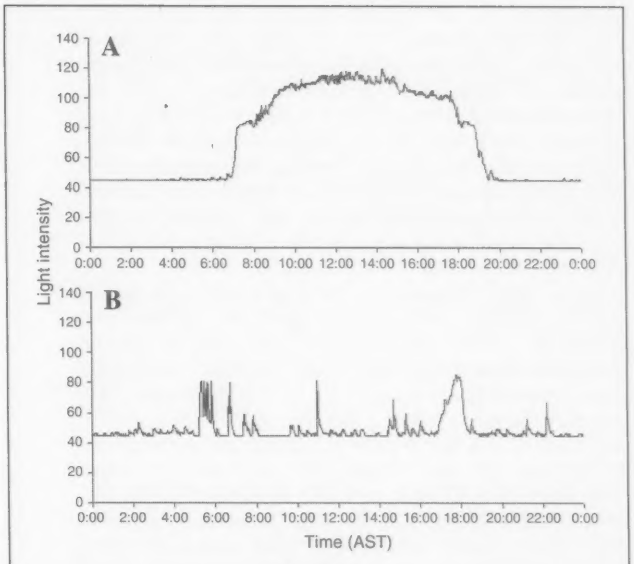

Figure 1

Examples of "good" and "bad" light curves. "Good" light curves (**A**) have smoothly sloping sunrise and sunset events. "Bad" light curves (**B**) do not have smoothly sloping sunrise and sunset events and produce outlying longitude and latitude estimates. The "good" light curve is from 2 March 2001 and the "bad" light curve is from the same tag on 10 March 2001. AST = Alaska standard time.

Results

All 14 tags, with the exception of one, functioned properly for the duration of the three experiments. The one exception, attached to a halibut *in situ*, was deployed for 234 days, but it provided data for only the first 42 days because the battery failed. Tracking durations for AMP (range: 42–479 days) were always equal to or greater than the tracking durations for TSP (range: 42–348 days) because the memory for the archival data filled up before the summary data memory.

In the tank experiment, TSP was a better estimator of longitude than AMP. TSP rejected fewer outliers and produced a higher percentage of days with longitude estimates (89.5%) than AMP (82.9%). Additionally, the mean longitude error magnitude for TSP (1.0° ±1.1° SD) was significantly smaller than that of AMP (2.0° ±3.2° SD) (t=5.63, df=650, P<0.0001). Longitude errors were larger from late-fall to mid-winter in both tags when estimated by AMP, but not TSP. The mean longitude bias of TSP (–0.12° ±1.5° SD) was significantly smaller than that of AMP (–0.64° ±3.7° SD) (t=2.3, df=650, P=0.0215). TSP was not significantly biased and AMP had a significant mean longitude bias.

In the tank experiment, TSP also produced a higher percentage of days with latitude estimates (88.2%) than AMP (81.6%). However, there was not a significant difference in the mean latitude error magnitude between TSP (4.2° ±5.1° SD) and AMP (4.4° ±4.2° SD) (t=0.36, df=641, P=0.7155). The mean positional bias of TSP (–0.02° ±6.7° SD) was not significantly different (t<0.0001, df=641, P=0.9730) from that of AMP (–0.08° ±6.1° SD) and neither software type had a significant mean positional bias.

In the fixed mooring experiment, TSP was a better estimator than AMP of longitude. In general, the tags produced fewer longitude estimates as depth increased, and at each depth, TSP generated more estimates than AMP (Fig. 2). The mean longitude error magnitude for both programs increased at greater depth (Fig. 3). The mean error magnitude of AMP and TSP estimates was not significantly different at 27 m and 57 m (P>0.50), but AMP estimates quickly degraded starting at 96 m (Fig. 3). For the tags at 96 m and 146 m, the mean error magnitudes for TSP estimates were significantly smaller (P<0.0001) than the AMP estimates of the same tags. The mean longitude biases of both AMP and TSP were generally to the west (positive values) of the actual position of the tags, except for AMP at 96 m (Fig. 3). In several cases, the mean biases were relatively small for both AMP and TSP, however both had large variances.

As with the longitude estimates in the fixed mooring experiment, the percentage of days with latitude estimates decreased at greater depths (Fig. 2). Unlike longitude, latitude was not estimated accurately by the tags. Mean latitude error magnitude was significantly smaller for TSP than for AMP at all depths, except 146 m (Fig. 3). The mean error magnitude for both AMP and TSP showed no relationship to increasing depth (Fig. 3). The mean latitude biases of the tags in the fixed mooring experiment were greater than the mean longitude biases, and the biases by AMP were more variable than those of TSP (Fig. 3). Like longitude in the fixed mooring experiment, latitude was not estimated at 146 m during the winter and spring. The time span without geolocation estimates was longer for latitude (242 days) than for longitude (165 days).

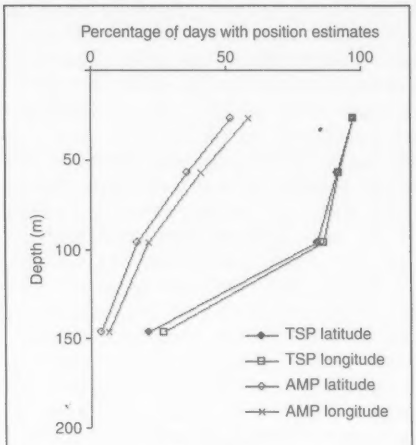

Figure 2

Percentage of days with longitude and latitude estimates as a function of depth in the fixed mooring experiment. Two programs, Argos Message Processor (AMP) and Time Series Processor (TSP), were used to calculate daily longitude and latitude.

In the wild fish experiment, four tags reported only to Argos satellites and geoposition was estimated from summary data by using AMP. The percentage of days with longitude estimates ranged from 0.0% to 2.3% (mean=1.1% ±1.0% SD), whereas the percentage of days with latitude estimates ranged from 0.0% to 1.5% (mean=0.6% ±0.7% SD). The other four tags were physically recovered and geoposition was estimated by using both summary data for AMP and detailed data for TSP. For AMP, the percentage of days with longitude estimates ranged from 0.0% to 12.0% (mean=5.8% ±5.9% SD), whereas the percentage of days with latitude estimates ranged from 0.0 to 7.9% (mean=3.4% ±3.5% SD). For TSP, the percentage of days with longitude estimates was higher, ranging from 9.9% to 32.3% (mean=19.7% ±9.4% SD) and days with latitude estimates ranged from 9.9% to 26.6% (mean=16.9% ±7.2% SD).

The mean error magnitude of the longitude estimates for AMP (n=4; 2.98° ±2.43° SD) was slightly larger than that of TSP (n=10; 2.23° ±2.38 SD°). However, the mean error magnitude of the latitude estimates for AMP (n=4; 2.76° ±1.59° SD) was approximately half that of TSP (5.65° ±4.11° SD). The mean longitude bias

for AMP (2.95° ±2.47° SD) was larger and to the east of that of TSP (–1.32° ±3.04° SD). The mean latitude bias was relatively small for both AMP (0.56° ±3.50° SD) and TSP (0.10° ±7.26° SD); however both had large variances and thus the estimates were not precise. In several cases, the longitude estimates were within one degree of the true position and there did not appear to be a pattern of over- or underestimating longitude.

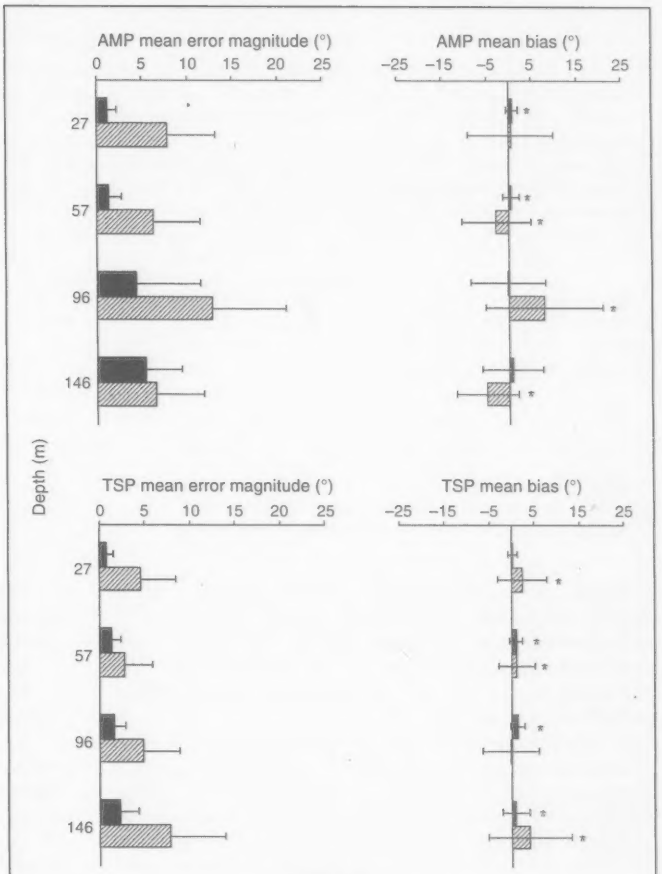

Figure 3

Mean (±SD) positional errors and bias in the fixed mooring experiment. Two programs, Argos Message Processor (AMP) and Time Series Processor (TSP), were used to calculate daily longitude (black bars) and latitude (hatched bars). Asterisks (*) indicate mean positional biases that were significantly different from zero in tests with two-way ANOVA. A negative bias indicates that a position estimate was either north or east of the known position, and a positive bias indicates that a position estimate was either south or west of the known position.

Discussion

Geolocation estimates determined from ambient light data in high latitudes is equally effective as in lower latitudes. Similar to results from previous geolocation evaluations (Welch and Eveson, 1999, 2001; Musyl et al., 2001; Teo et al., 2004), our longitude estimates were in general more accurate and precise than latitude estimates. Therefore, longitude estimation by light is a promising technique for discerning large-scale movement of demersal fishes in coastal Alaska, but latitude estimation determined from light data only will not be adequate for these purposes.

This study was unique in testing light-based geolocation in depths greater than 60 m. The results demonstrate the importance of evaluating geolocation by light for the entire depth range of the species of interest. Testing only in the near-surface waters would be misleading because the percentage of days with estimates from tags at shallower depths was much greater than the percentage of days with estimates from tags at greater depths—the depths which halibut most frequently inhabit (Seitz et al., 2003).

The accuracies of the longitude estimates in this study were comparable to those at lower latitudes and similar water depth. Errors are discussed in linear distance (Table 1) to account for the fact that a degree of longitude varies with latitude and to facilitate comparisons to previous studies. The longitude errors from the tank experiment were generally similar to the errors produced in a comparable experiment where tags were placed on a stationary mooring at a depth of 10 m (Welch and Eveson, 1999). The tags submerged at deeper depths in the fixed mooring experiment also showed a longitude error magnitude similar to that of location estimates from tags in the offshore region of the Gulf of Alaska at 50°N, 145°W (Musyl et al., 2001; Welch and Eveson, 2001). The longitude biases were only slightly larger than those from tags on a stationary mooring near Hawaii (Musyl et al., 2001).

The minimum movement of a fish that was discerned by light-based geolocation in our experiment is the absolute sum of the error magnitude and bias. The sum of the error magnitudes and biases of TSP were generally smaller than those of AMP; therefore TSP was a better estimator of light-based geoposition than AMP and can be used to discern movement at a finer scale. The tank and fixed mooring experiments indicated that longitude estimation by TSP is able to discern movements of approximately ±200 km for depths as great as 150 m and AMP is able to discern east-west movements of approximately ±350 km at 150 m deep. Geolocation by light will be able to discern the large-scale movements

Table 1

Linear distance of mean error magnitude for the tank, fixed mooring, and wild fish experiments. Longitude and latitude were calculated from light intensity data collected by pop-up archival transmitting tags in two programs, Argos Message Processor (AMP) and Time Series Processor (TSP). Mean error magnitude was calculated by averaging the absolute value of the difference of the true position and the estimated position of the tag for each day of the experiment. Total error was the vector distance from the known location of the tag when longitude and latitude errors were combined. The great circle formula was used to convert angular errors to linear distances.

			AMP			TSP		
Experiment	Tag	Depth (m)	Longitude (km)	Latitude (km)	Total error (km)	Longitude (km)	Latitude (km)	Total error (km)
Tank	00-0740	0	139.1	500.9	519.8	62.9	500.9	504.8
Tank	00-0741	0	83.5	480.8	488.0	48.4	445.2	447.8
Mooring	00-0822	27	66.2	873.7	876.2	41.7	505.3	507.0
Mooring	00-0826	57	74.6	696.8	700.7	74.6	310.5	319.4
Mooring	00-0806	96	241.5	1421.3	1441.7	89.6	540.9	548.3
Mooring	00-0824	146	299.3	726.8	786.0	123.5	871.5	880.2
Wild fish	All tags	90–202	165.8	307.2	362.6	124.1	628.9	392.0

of Pacific halibut because this species performs spawning migrations of over 1100 km (Loher[5]). Additionally, with recovery rates as high as 50% in area-specific conventional tagging experiments (Kaimmer, 2000), TSP can could be used for a large portion of tag recoveries in future experiments.

At the largest scale, we were able to discern with confidence whether the wild Pacific halibut in this study were in the Gulf of Alaska or Bering Sea. Individual estimates were subject to occasional large errors and therefore caution should be practiced when using these estimates to represent the true position of fish. Examining patterns in estimates is more useful for determining locations. To reach the Bering Sea (west of 157°W), a Pacific halibut would have to migrate from the Gulf of Alaska through False Pass (163.5°W), which is the eastern-most connection between the two areas. The wild Pacific halibut in our study appeared to remain within the Gulf of Alaska, because fewer than 5% of the longitude estimates were to the west of 163.5°W, and those appeared to be erroneous because adjacent estimates did not consistently corroborate them. Trends in longitude estimates did not provide sufficient evidence to indicate that any of the wild Pacific halibut swam to the Bering Sea.

A variety of uncontrollable factors can cause intrinsic and extrinsic errors in geolocation estimates. The predominant source of intrinsic error is refraction in the earth's atmosphere that is caused when light travels through the atmosphere and is bent by air and other molecules (Schaefer and Liller, 1990). This error limits the absolute accuracy of the estimates to a constant 0.32° longitude and a minimum of 0.7° latitude (Hill and Braun, 2001). Extrinsically, light levels may be drastically influenced by changing external conditions, such as waves, water turbidity, diving behavior of the animal, biofouling, and cloud cover (Metcalfe, 2001). In particular, the Alaska coastal region frequently experiences large changes in weather systems that change cloud cover and sea-state on a daily, or even hourly, basis. One final consideration for errors is that accurate location estimates rely on unobstructed horizons. If the horizon is obstructed, such as by the mountains surrounding the coast of Alaska, it alters the time(s) of apparent sunrise (and sunset), thus affecting geolocation estimates. The tank experiment was conducted in a deep, north-south fjord whose walls obstructed the horizon, and the fixed mooring experiment was adjacent to an island on the east and to steep coastal mountains to the west. Undoubtedly, these false horizons accounted for part of the errors and bias.

One shortcoming discovered in the fixed mooring experiment was a conspicuous gap in longitude and latitude estimates from December to June at 146 m. This six-month gap was probably the result of low ambient light levels during the winter associated with high latitudes. It is unknown why the gap lasted into the summer when ambient light drastically increased. However, for practical application in studies of Pacific halibut migration, light-based geolocation estimates will capture some individual migrations to the spawning grounds as some Pacific halibut begin migrating in October and arrive on the continental slope by early November (Seitz et al., 2003).

We may be able to increase the number of location estimates with some fine-tuning of both software types. Several days were rejected because of poor light readings. However, some days had smoothly sloping sunrise and sunset events that appeared to be sufficient for accurate geolocation estimates, but the software mis-

[5] Loher, T. 2005. Personal commun. Int. Pac. Halibut. Comm, PO Box 95009, Seattle, WA 98145-2009.

identified sunrise and sunset. This misidentification typically occurred because there were occasional aberrant light readings. The geolocation software identified these as sunrise, sunset, or both, and therefore gave bogus position estimates. There is an option to override these aberrant sunrise and sunset times when using TSP because the software allows manual selection of sunrise and sunset. For our study, we opted not to do this because we did not want to introduce subjectivity into sunrise and sunset times. We suggest that the software be modified by the manufacturer to select the next best times for sunrise and sunset so that the investigator may reject aberrant light readings and yet allow the software to objectively choose sunrise and sunset.

In future studies, we hope to improve geoposition estimates by statistically filtering (Sibert et al., 2003) or smoothing longitude estimates and by incorporating additional sensor data. For example, in conjunction with light data, tag-measured sea-surface temperature (SST) can be compared to remotely sensed SST, to significantly improve geolocation estimates (Teo et al., 2004). In the case of demersal fish that rarely, if ever, visit the sea surface, maximum daily depth can be used as representative of the total water depth in the region. We can compare the maximum daily depth sampled by an electronic tag to existing bathymetry data to estimate possible daily positions of the fish. We can then combine the geolocation estimated by light-level information with the depth information to yield a most plausible track of daily positions.

Accurate description of the movement of fish is the cornerstone of sound management plans for ensuring sustainable fisheries in the future (Hunter et al., 2003). Longitude estimation determined from ambient light data may be used to examine large-scale movements of demersal fish in high latitudes. There are several types of electronic tags—some designed for fish as small as 15 cm (Arnold and Dewar, 2001). Using this technique, we can describe large-scale spatial dynamics and migration of several commercially important demersal fish species.

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Abundance and distribution of whale sharks (*Rhincodon typus*) in the northern Gulf of Mexico

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Abstract—Information on the seasonal abundance and distribution of whale sharks (*Rhincodon typus*) is largely unknown throughout range of the species. Between 1989 and 1998, three spatially and temporally intensive aerial surveys were conducted by the National Marine Fisheries Service, Mississippi Laboratories that provided information on seasonality, distribution, and aggregations of whale sharks in the northern Gulf of Mexico. Transects totaling 89,369 km were surveyed over the course of the study and a total of 119 whale sharks were counted during 81 sighting events. There was no statistical difference in the sightings per unit of effort (SPUE) of whale sharks between the eastern and western continental slope waters of the Gulf of Mexico. In the continental slope waters of the eastern Gulf of Mexico, whale sharks were more abundant during the summer than in the winter. In the western Gulf of Mexico, whale shark SPUE was significantly greater in the summer than during the fall or winter; there was no significant difference between summer and spring. There was also no significant difference in whale shark SPUE among spring, fall, and winter in the western Gulf of Mexico. Aggregations of whale sharks were seen only during the winter and summer, and there were significantly more individuals per aggregation during the summer. The largest aggregation of whale sharks observed during the study consisted of 23 individuals.

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Whale sharks (*Rhincodon typus*) are distributed in all tropical and subtropical marine waters of the world, with the exception of the Mediterranean Sea (Compagno, 1984). This species is considered vulnerable to extinction according to the World Conservation Union (IUCN)[1] partly because of a lack of information pertaining to its life history. Although the seasonality of whale sharks has been examined in two geographically discrete areas (Taylor, 1996; Duffy, 2002), no information exists for the seasonal distribution or relative seasonal abundance of this species over a broad spatial scale. The paucity of such information is probably attributable to logistical difficulties associated with collecting required data or to the expense of surveying large areas.

Whale sharks aggregate in areas of high biological productivity, and seasonal abundance of whale sharks could result from increased localized prey abundance. Whale sharks feed on a variety of organisms including invertebrates and teleosts (Compagno, 1984). Unlike basking (*Cetorhinus maximus*) and megamouth (*Megachasma pelagios*) sharks, which passively filter prey from the water column, whale sharks are capable of suction filter feeding (Colman, 1997). Although this feeding strategy enables whale sharks to capture a wider range of prey in terms of size, mobility, and diversity than other filter feeding elasmobranchs, this feeding strategy requires dense aggregations of prey in order for whale sharks to meet their energetic demands (Compagno, 1984). Feeding aggregations of whale sharks have been reported in the Atlantic, Indian, and Pacific Oceans and specifically in the waters off Belize, Western Australia, the Galapagos Islands, Mexico, New Zealand, and Thailand (Taylor, 1996; Clark and Nelson, 1997; Colman, 1997; Eckert and Stewart, 2001; Heyman et al., 2001; Wilson et al., 2001; Duffy, 2002).

The whale shark was first described in 1828 from a type specimen collected off the coast of South Africa (Penrith, 1972). The first record of a whale shark in the western North Atlantic Ocean was not reported until 1902 and it was 1937 before this species was documented in the Gulf of Mexico (Gudger, 1939; Baughman and Springer, 1950; Breuer, 1954). Since 1937 several authors have reported sightings of whale sharks in the Gulf of Mexico (Gudger, 1939, 1941; Baughman, 1947, 1950, 1955; Gunter and Knapp, 1951; Breuer, 1954; Springer, 1957; Clark and von Schmidt, 1965; Hoffman et al., 1981; Hoffmayer et al., 2005). However, these reports are restricted to spatially discrete areas, and most are primarily anecdotal and largely based on isolated observations of few individuals. In the present study we report the seasonality, rela-

[1] The World Conservation Union. 2005. http://www.redlist.org [accessed 5 January, 2006].

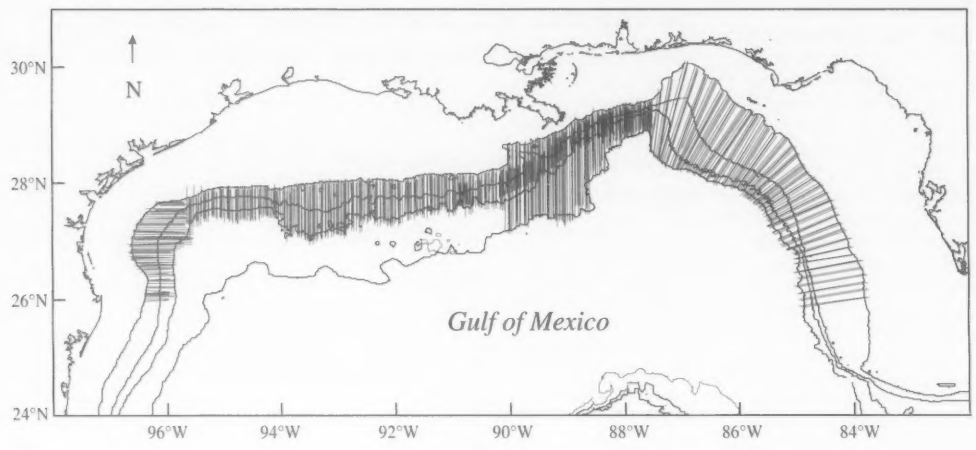

Figure 1

Transect lines surveyed by aircraft during three aerial studies conducted in the northern Gulf of Mexico from 1989 to 1998. Note that some lines overlap others, particularly in the eastern Gulf of Mexico. Bathymetric contours represent the 100-, 500-, 1000- and 2000-meter contours.

tive seasonal abundance, distribution, and aggregations of whale sharks observed in the northern Gulf of Mexico during three spatially and temporally intensive aerial surveys conducted by the National Marine Fisheries Service, Mississippi Laboratories.

Materials and methods

Between 1989 and 1998, three aerial surveys were conducted in the northern Gulf of Mexico with a DeHavilland Twin Otter turbine engine aircraft. The primary objective of one of these surveys, referred to as the Upper Continental Slope (UCS) Survey, was to examine species composition, distribution, and seasonality of cetaceans in the north-central Gulf of Mexico (Mullin et al., 1994). The purpose of the other two surveys, referred to as the Gulf of Mexico Cetacean Studies I (GulfCet I) and Gulf of Mexico Cetacean Studies II (GulfCet II) (Mullin and Hoggard[2]) surveys, was to assess possible impacts of petroleum industry activities on cetaceans and sea turtles in the Gulf of Mexico. Standard line-transect sampling methods were used for each survey (Buckland et al., 1993). Surveys were flown at a constant altitude and air speed of 229 m and 200 km/h, respectively. The aircraft was modified with a Plexiglas observation bubble on the port and starboard sides of the fuselage to permit an unobstructed view of the area along transect lines and a lateral view to each horizon. When fauna of interest were sighted, the pilot circled the area until all observed fauna were identified to the lowest possible taxa and the latitude and longitude of the sighting and numbers of conspecifics sighted were recorded. All survey effort was limited to waters associated with the continental slope in Beaufort sea states less than 4 and restricted to areas within the United States Exclusive Economic Zone (EEZ; Fig. 1). For all analyses and discussion, seasons were defined as spring (April–June), summer (July–September), fall (October–December), and winter (January–March).

The UCS survey was conducted from the summer of 1989 through the spring of 1990 and was carried out during all four seasons. The study area was located in the central northern Gulf of Mexico along the continental shelf break (~200-m isobath) south of the Mississippi River Delta and extended from the DeSoto Canyon (87°00′W) to the western edge of the Mississippi Trough (90°05′W). GulfCet I surveys occurred from 1992 to 1994 over continental slope waters in the western Gulf of Mexico between the United States and Mexico border (25°57′N) and the Mississippi–Alabama border (88°25′W) and were conducted during all four seasons (Mullin et al., 2004). GulfCet I transects began at the 100-m isobath and extended to the 1000-m isobath west of 90°00′W, and to the 2000-m isobath east of 90°00′W. GulfCet II surveys were conducted only during the winter and summer between 1996 and 1998 in the northeastern Gulf of Mexico and covered continental slope waters (100–2000 m deep) and a portion of the continental shelf (Mullin and Hoggard[2]). The entire spatial range of the three areas was surveyed within each season of operations. Because of the spatial overlap of the UCS and GulfCet II surveys, the central northern Gulf of Mexico and the western Gulf of Mexico were treated as a single region, referred to as "the western

[2] Mullin, K. D., and W. Hoggard. 2000. Visual surveys of cetaceans and sea turtles from aircraft and ships. *In* OCS Study MMS 96-0027, vol. II, Cetaceans, sea turtles and seabirds in the northern Gulf of Mexico: distribution, abundance and habitat associations (R. W. Davis, W. E. Evans, and D. Würsig, eds.), p. 111–172. Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA 70123.

Table 1

Summary of survey effort, number of whale shark (*Rhincodon typus*) sightings, and sightings per unit of effort (SPUE) by region, season, and survey. UCS=upper contintental survey; GulfCetI=Gulf of Mexico Cetacean Studies I; GulfCet II=Gulf of Mexico Cetacean Studies II.

Survey and region covered	Season	Effort (km)	Number of sharks	SPUE
UCS—western Gulf of Mexico	winter	4382	1	0.23
	spring	7615	8	1.05
	summer	5321	14	2.63
	fall	3275	0	0.00
GulfCet I—western Gulf of Mexico	winter	12,645	13	1.03
	spring	12,645	20	1.58
	summer	12,942	43	3.32
	fall	11,756	7	0.60
GulfCet II—eastern Gulf of Mexico	winter	8348	3	0.36
	summer	10,440	10	0.96

Gulf of Mexico," in this article. Mobile Bay, Alabama (88°00′W) was considered to be the dividing line between the eastern and western Gulf of Mexico.

Sightings per unit of effort (SPUE) were calculated to correct for unequal effort among regions by dividing the number of sightings per season by the total survey effort during the same season and then multiplying the resulting value by 1000. Because aerial surveys were limited to summer and winter in the eastern Gulf of Mexico, data from these two seasons in this region were compared (by using a t-test) to data collected during surveys in the same two seasons in the western Gulf of Mexico to determine if mean whale shark SPUE was significantly different between the two areas. To determine if there was a season of peak whale shark SPUE in the western Gulf of Mexico a one-way analysis of variance (ANOVA) and the Student-Newman-Keuls test were employed. The Mann-Whitney test was used to determine if there was a significant relationship between season and number of individuals per aggregation. This test was selected because of the non-Gaussian distribution of these data. The location of each whale shark sighting was plotted on navigational charts, produced by the National Oceanic and Atmospheric Administration (Chart numbers 11006, 11300, 11340), to examine the associations of whale sharks with bathymetric features such as reefs and salt diapirs. Statistical tests were preformed according to the methods of Zar (1999) at a significance level of $P \leq 0.05$.

Results

Transects totaling 89,369 km were surveyed over the course of the study (Table 1). A total of 119 whale sharks were counted during 81 sighting events (Fig. 2). There was no statistical difference in the SPUE of whale sharks between the eastern and western continental slope waters of the Gulf of Mexico (t-test, df=4, t-value=1.06, P=0.35). Because survey effort in the eastern Gulf of Mexico was limited to summer and winter, it was not possible to quantitatively analyze whale shark seasonality in this region. However, results indicated that whale sharks are more abundant in the eastern Gulf of Mexico during the summer (SPUE=0.96) than in the winter (SPUE=0.36). There was a statistically significant difference in whale shark SPUE among seasons in the western Gulf of Mexico (ANOVA, df=7, F-ratio=12.97, P=0.02). The Student-Newman-Keuls test indicated that whale shark SPUE was significantly greater in the summer ($\bar{x}$= 2.98, SD=0.49) than during the fall ($\bar{x}$=0.30, SD=0.18) or winter ($\bar{x}$=0.63, SD=0.32). However, there was no significant difference between summer and spring ($\bar{x}$=1.32, SD = 0.38). There was no significant difference in whale shark SPUE among spring, fall, and winter.

Of the 119 whale sharks sighted over the course of the study, 45 were observed in aggregations—an aggregation being defined as the presence of two or more whale sharks in close proximity to one another. Seven aggregations, ranging in size from 2 to 23 individuals, were observed. Aggregations of whale sharks were seen only during the winter and summer and there were significantly more individuals per aggregation during the summer (Mann-Whitney test, W=12.0, P=0.05). Sixty-two percent (n=74) of whale sharks were not observed in association with conspecifics.

The majority of whale sharks observed were not associated with discrete areas of high bathymetric relief. Thirty-four of the whale sharks sighted were in close proximity to relatively small, high relief diapiric features dominated by coralline algae (Rezak et al., 1990); Ewing Bank (28°06′N, 91°02′W), Bright Bank (27°53′N, 93°18′W) and 28 Fathom Bank (27°55′N, 93°26′W). Of the seven aggregations observed during the surveys, three were associated with the aforementioned banks including the aggregation consisting of 23 individuals. The area of highest whale shark abundance was located in an area of approximately 16,800 km^2 and

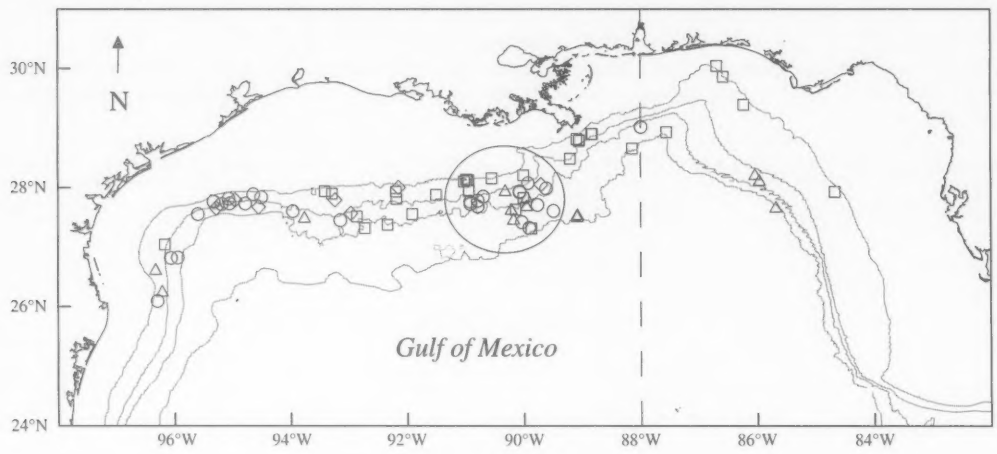

Figure 2

Locations (n=81) of whale sharks (*Rhincodon typus*) observed during aerial surveys in the northern Gulf of Mexico from 1989 to 1998. Dashed line demarks the separation between the eastern and western Gulf of Mexico as defined in our study. Area contained within the circle indicates region of highest observed whale shark abundance. Bathymetric contours represent the 100-, 500-, 1000- and 2000-meter contours. Location and season of sighting symbols: △ = winter, ○ = spring, □ = summer, ◇ = fall.

the center of their distribution was approximately 140 km southwest of the Mississippi River Southwest Pass (Fig. 2). Twenty-seven whale sharks were observed in this region over a four-year period.

Discussion

We observed whale sharks throughout the year in the Gulf of Mexico, and our study is the first to identify a broad region where whale sharks are present during all seasons and where they are perhaps resident throughout the year. The highest SPUE values that we observed occurred during the summer. Therefore, given the reported seasonality of whale sharks in the western Caribbean Sea (Heyman et al., 2001) and southeastern Gulf of Mexico (Gudger, 1941), it is reasonable to assume that a portion of the population migrates into the northern Gulf of Mexico during the spring and in winter moves into lower latitude waters, such as the Bay of Campeche and waters off the coast of Cuba. The only entrances to the Gulf of Mexico are through the Yucatan Channel and the Straits of Florida; therefore research with telemetry and satellite tagging in these regions would help determine the timing and routes of whale shark migrations and the period of residency within the Gulf of Mexico.

Whale sharks are more abundant in the western than in the eastern Gulf of Mexico. However, because the aerial surveys were limited to two seasons in the eastern Gulf of Mexico, little can be inferred from our data, except confirmation of the presence of whale sharks in the eastern Gulf of Mexico during the winter and the addition of summer to the seasonality of occurrence in this region. Because the survey reported in our study focused solely on continental slope waters, it is possible that whale sharks in the eastern Gulf of Mexico use continental shelf waters to a greater extent and, thus, were outside of the sampled area. Despite extensive effort over the broad upper continental slope off the west coast of Florida, no whale sharks were observed south of 27°38′N. However, at higher latitudes, 13 individuals were sighted in continental slope waters at depths ranging from 70 to 180 m. Because the upper continental slope is broader in the eastern than in the western Gulf of Mexico, it is possible that whale shark distribution in the eastern Gulf of Mexico is more diffuse than would be expected, especially if this species is associated with steep bathymetric relief, which promotes upwelling of nutrient rich waters. During our study, two whale sharks were observed at the head of the DeSoto Canyon, an upwelling area south of the Florida panhandle. A large aggregation (30–100 individuals) was found in this same area by Hoffmayer et al. (2005).

In the western Gulf of Mexico, whale sharks were observed in all sampled depth strata, and the spatial distribution of sightings was fairly continuous along the continental slope from Mobile Bay (88°00′W) to the United States/Mexico border (96°30′W; Fig. 2). Seasonally, whale sharks were present year round in the western Gulf of Mexico, except between 94°00′W and 95°35′W where they were observed only during spring and fall. Bimodality in seasonal occurrence in this region could be attributed to seasonal fluctuations in biological productivity and, thus, to prey availability resulting from ephemeral mesoscale phenomena such as Loop Current eddy formation, current reversals, and coastal jetting. For example, in the western Gulf of Mexico the Texas Current is capable of

generating localized upwelling on the continental shelf break, thus increasing primary productivity and the availability of prey species (Sahl et al., 1993). However, the Texas Current occasionally flows in a direction opposite to its normal eastward course because of wind forcing (Sahl et al., 1997). Such a reversal of direction in the Texas Current could affect productivity in this area and thus influence the seasonal abundance of whale sharks in this region. Given the stochastic nature of the physical oceanography of this region, additional research will be needed to determine if whale sharks make limited use of this area during discrete times of the year or if they are in fact present year round.

From observations made by commercial mariners in transit between the southern tip of Florida and unidentified ports in Texas, Gudger (1941) reported sightings of 68 whale sharks from a circular area in the north-central Gulf of Mexico with a diameter of approximately 280 km; however no specific locations were given. He concluded that the density of whale sharks in this area must be related to high prey densities. The area of highest regional abundance during the present study occurred in a circular area, bounded by 89°30′W and 91°00′W longitude, and having a diameter of approximately 165 km (Fig. 2). Three aggregations of between 30 and 100 whale sharks in this same area were reported by Hoffmayer et al. (2005). The safety fairway used by shipping traffic transiting between the eastern and western Gulf of Mexico crosses this area. It is probable, therefore, that the observations of whale sharks by commercial mariners reported by Gudger (1941) were in the same area. Because of nutrient loading from the Mississippi and Atchafalaya rivers, primary productivity is higher in this region of the Gulf of Mexico than in any other region (Lohrenz et al., 1999) and may explain the high localized abundance of whale sharks in this region. Other highly productive areas where whale sharks are known be present in relatively large numbers include Ningaloo Reef, Australia, and Gladden Spit, Belize (Taylor, 1996; Heyman et al., 2001).

The sighting of 23 whale sharks on 9 August 1993 was the largest aggregation observed during our study. The sharks, which were observed for about 35 minutes, were distributed over an area of approximately 2.6 km^2. Coral spawning occurred on 9 August 1993 at the East Flower Gardens (27°55′N, 93°36′W; Gittings[3]) which is approximately 33 km due west of the location of the aggregation sighting. A similar relationship between coral spawning events and increased localized abundance of whale sharks has also been noted to occur off the coast of Western Australia (Taylor, 1996). Future efforts should examine the relationship between annual coral spawning events and whale shark occurrence near the East Flower Gardens to determine if there is an annual migration of whale sharks to this area.

[3] Gittings, S. R. 1993. Personal commun. Science Program Manager, NOAA Office of National Marine Sanctuaries. 1305 East West Hwy, Silver Springs, MD 20910.

There are inherent difficulties associated with examining the seasonality of marine organisms using aerial surveys. This is particularly true when the species of interest is not obligated to surface waters where visual observations can be made. Because the whale shark is not a surface obligate species, factors such as changes in feeding behavior resulting from seasonal variability in the vertical distribution of prey species could have introduced significant bias into our sighting data, subsequent analyses, and data interpretation. We assumed that no differences exist among seasons in the amount of time whale sharks spend at or in close proximity to the surface. Using telemetry and archival tags, Gunn et al. (1999) determined that whale sharks spend 17–53% of their time at the surface during daylight hours off the coast of Australia. Over periods ranging from 28–1144 days, Eckert and Stewart (2001) tracked vertical movements of whale sharks through the water column in the Sea of Cortez using satellite tags. They concluded that during all seasons whale sharks spend greater than 80% of their time at depths of 10 m or less during all seasons—depth well within the photic zone of continental slope waters of the Gulf of Mexico. The findings of both Gunn et al. (1999) and Eckert and Stewart (2001) support our assumption.

Due to the economic value of their meat, fins, and liver oil, whale sharks have recently been designated as vulnerable to harvesting-induced extinction by the IUCN (Stewart and Wilson, 2005). Furthermore, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) has placed the whale shark under Appendix II, which limits the trade of whale shark products among cooperating nations (Stewart and Wilson, 2005). Within the United States EEZ, the retention of whale sharks caught commercially or recreationally is prohibited (NMFS, 1993). However, because whale sharks are highly migratory and their movements cross numerous boundaries, detailed information on their abundance and seasonal distribution is needed to ensure their well being.

Acknowledgments

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Effects of a simulated fishing moratorium on the stock assessment of red porgy (*Pagrus pagrus*)

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Abstract—Much of the information available on the population status of a harvested fish species is obtained from landings data. When fishing restrictions are in place, fishery-dependent data are reduced and assessments rely more heavily on fishery-independent data. Stock assessments of red porgy (*Pagrus pagrus*) have shown a declining population and have led to a number of management measures, including a moratorium on fishing this species. To investigate how a lack of fishery-dependent data during a moratorium would affect stock assessment results for red porgy, we conducted simulations representing a range of periods of moratorium. As data were removed from the model, stock status indicators and projections became increasingly variable. Projections estimated that a 12-year moratorium would be needed for stock rebuilding, but simulations showed that uncertainty surrounding stock assessment estimates would increase after three years without fishery-dependent data. Unless additional data are collected during periods of strict fishing regulations, it may be difficult to accurately assess the length of time needed for the stock to rebuild and to assess the population status.

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For commercial or recreational fisheries, a large portion of the information available for assessment of the population status of a species is obtained during harvesting operations. When harvest restrictions are in place, fishery-dependent data are reduced and assessments become more reliant on fishery-independent data. During a moratorium, harvest ceases completely and new methods may be required to assess the status of the stock. It is assumed that stock assessment results accurately portray the current population and that these results are used in policy decisions affecting future stock status. However, stock assessment results are not solely a product of the population being assessed, but are also a function of stock status, data sources, and sample size. Although most stock assessments include close evaluation of data sources, few assessments include the quantification of potential effects of changes in fishery-dependent data as a byproduct of changing harvest restrictions. We therefore investigated the effects of the reduced availability of fishery-dependent data on stock assessment results and management decisions.

To accomplish this goal, we conducted model simulations for red porgy (*Pagrus pagrus*) that is found off the coast of the southeastern United States from North Carolina to Florida. This reef-associated fish is an important resource for commercial and recreational fisheries (Huntsman et al., 1978; Low et al., 1985). Red porgy have an extensive native range and inhabit coastal waters on both sides of the Atlantic Ocean in both hemispheres (Pajeulo and Lorenzo, 1996; Labropoulou et al., 1999; Hood and Johnson, 2000). They are associated with live-bottom reef habitats on rocky outcroppings and therefore have a patchy distribution off the southeastern United States (Grimes et al., 1982). Red porgy are protogynous hermaphrodites; females dominate the smaller size classes, and males occur at all ages (Manooch, 1976). Females generally reach maturity from age-1 to age-2 at approximately 300 mm total length, and the majority of red porgy age-5 and older are mature males (Hood and Johnson, 2000).

Red porgy have been harvested extensively by three major fisheries (Fig. 1): commercial, recreational, and a fishery comprising large-scale charter boats called "headboats" (Huntsman et al., 1978). All three fisheries use mainly hook-and-line gear and target a wide variety of temperate reef fishes (Chester et al., 1984), not exclusively red porgy. In the early 1980s, the red porgy stock began showing signs of decline (Collins and Sedberry, 1991; Vaughan et al., 1992). As the stock decline became more evident, the minimum size limit was raised (Table 1) by the South Atlantic Fishery Management Council (SAFMC), the group mandated with managing red porgy and other fish off the coast of North

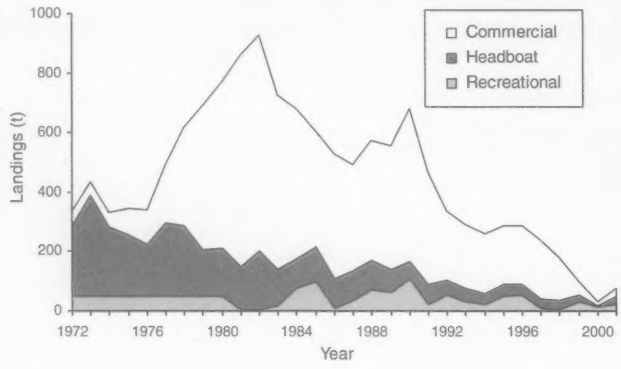

Figure 1

Landings (in metric tons) of red porgy (*Pagrus pagrus*) off the coast of the southeastern United States for the commercial, recreational, and headboat fishery sectors from 1972 through 2001.

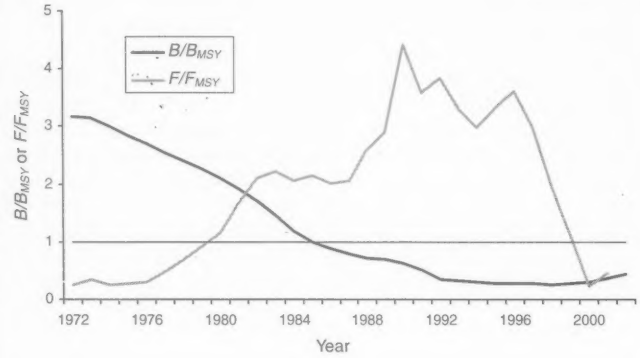

Figure 2

Relative biomass (B/B_{MSY}) and relative fishing mortality (F/F_{MSY}) for red porgy (*Pagrus pagrus*), as estimated in SAFMC (see Footnote 3 in the general text). The horizontal line represents $B=B_{MSY}$ and $F=F_{MSY}$.

Carolina, South Carolina, Georgia, and eastern Florida (SAFMC[1]). However, red porgy abundance continued to decrease (Vaughan and Prager, 2002), such that an emergency moratorium was put into place (Table 1) prohibiting the harvesting of red porgy by all fishery sectors. Following debate on the actual severity of the population decline and uncertainty surrounding the stock assessment, the moratorium was relaxed a year later to a seasonal closure, a recreational bag limit, and a commercial bycatch allowance (Table 1; SAFMC[2]). A recent stock assessment (Fig. 2; SAFMC[3]) identified this red porgy stock as having low biomass, but not as being currently overharvested. The strict harvest regulations applied to red porgy led to SAFMC concerns regarding the ability of scientists to accurately assess a population under a moratorium when fishery-dependent data are unavailable.

[1] SAFMC (South Atlantic Fishery Management Council). 1991. Final, amendment number 4, regulatory impact review, initial regulatory flexibility analysis and environmental assessment for the fishery management plan for the snapper grouper fishery of the South Atlantic region, 99 p. + appendices. South Atlantic Fisheries Management Council, One Southpark Circle, Suite 306, Charleston, SC 29407.

[2] SAFMC (South Atlantic Fishery Management Council). 2000. Final, amendment number 12 to the fishery management plan for the snapper grouper fishery of the South Atlantic region, 159 p. + appendices. South Atlantic Fishery Management Council, One Southpark Circle, Suite 306, Charleston, SC 29407.

[3] SAFMC (South Atlantic Fishery Management Council). 2002. Southeast Data, Assessment, and Review (SEDAR) stock assessment for red porgy, 39 p. South Atlantic Fishery Management Council, One Southpark Circle, Suite 306, Charleston, SC 29407.

Table 1

History of fishing regulations for red porgy (*Pagrus pagrus*) applied to both commercial and recreational fisheries, unless otherwise specified.

Regulation period	Regulation details	Regulation period	Regulation details
To 1992	No size, bag, or trip limits or closures	Sept 1999 to Aug. 2000 (moratorium)	No landings permitted
Jan 1989 to present	Trawl gear banned	Aug 2000 to present (Amendment 12)	356-mm minimum size limit; 1-fish recreational bag limit; Jan–Apr commercial closure; 22.7-kg commercial trip limit
1992 to Jan 1999	305-mm minimum size limit		
Feb 1999 to Aug 1999 (Amendment 9)	356-mm minimum size limit; 5-fish recreational bag limit; Mar–Apr commercial closure		

Red porgy is a relatively well-studied species; more than 30 years of information are available. However, the majority of the data for this species is a direct result of fishing operations. Fishery-dependent data for red porgy include landings (number of fish) from commercial, recreational, and headboat fisheries, as well as large sample sizes of lengths from these fisheries (Table 2; Huntsman et al., 1978; Low et al., 1985; NMFS[4]). The headboat fishery also provides an abundance index based on catch-per-unit-of-effort data. Although fishery-dependent data provide large sample sizes and a relatively long time series, there are a number of problems associated with this information source. Fishery-dependent statistics have been affected by frequent changes in regulations, economics, technology, and gear (Collins, 1990) that may cause difficulties for comparisons of landings, abundance indices, or lengths among years. Moreover, harvest data have inherent biases due to the nature of the fishery, which attempts to maximize catch, selects fishing areas nonrandomly, and targets larger size classes of fish.

In an attempt to compensate for some of the biases potentially present in harvest data, the National Marine Fisheries Service (NMFS) instituted the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program in 1979. During this annual survey, fishery-independent data are collected on a variety of reef fishes in waters from North Carolina to Florida (Collins, 1990; Harris and McGovern, 1997). In the MARMAP survey standardized gear types are used and known amounts of effort are applied to sample randomly selected sites between May and August (Collins, 1990), during which information on length, weight, age, sex, fecundity, and level of maturation are collected. An abundance index is also calculated for each gear type.

[4] NMFS (National Marine Fisheries Service). Fisheries Statistics Division. 2005. Website: http:www.st.nmfs.gov/st1 [accessed on 31 January 2005].

The MARMAP survey and other well-designed fishery-independent surveys are extremely useful for stock assessments because standardized gears are used with known efforts in documented locations, which constitute a statistically valid experimental design that facilitates comparisons among years, areas, and gear types (Collins and Sedberry, 1991). However, the MARMAP survey does not provide information on harvesting, and the survey's sampling methods are inherently different from fishery-dependent sources. Therefore, MARMAP data cannot serve as an absolute substitute for fishery-dependent information in existing stock assessment strategies. In addition, MARMAP sample sizes are much smaller than those from fishery-dependent sources, particularly for length-frequency data; 92% of samples for length-frequency estimates were obtained from fishery-dependent sources (Table 2).

In a highly restricted or closed fishery where fishery-dependent data are limited, information from fishery-independent sources may be the only data available to managers. This decreased amount of data could affect stock assessment results, including the estimation of stock status indicators and benchmarks used in management. It is therefore important to understand how to best use both fishery-independent and fishery-dependent data in assessments of red porgy and other species, both in unrestricted and heavily restricted fisheries.

During a moratorium or other period of strict regulation, the reduction in fishery-dependent data may increase variability surrounding status indicators and management benchmarks. We quantified the increase in variability for red porgy by using stock assessment model simulations and projections, and we identified how the uncertainty surrounding estimates could affect management decisions. By evaluating the effects of a lack of data before harvest restrictions are put in place, managers will be able to identify future data needs, improving their ability to assess and manage species of concern.

Table 2

Sample sizes for estimation of lengths and ages of red porgy (*Pagrus pagrus*) from fishery-independent (Marine Resources Monitoring, Assessment, and Prediction, [MARMAP] survey) and fishery-dependent (commercial and headboat fisheries) sources. The stock assessment model covered 1972–2001; therefore "model years" is equal to a span of 30 years.

Data source	Samples	Years	Samples per model year	Percentage
Lengths				
MARMAP	11,649	17	388	8.2
Commercial	81,625	26	2721	57.4
Headboat	49,012	30	1634	34.4
Total	142,286		4743	
Ages				
MARMAP	5274	13	176	57.5
Commercial	1250	4	42	13.7
Headboat	2645	4	88	28.8
Total	9169		306	

Materials and methods

Stock assessment model

The simulations to determine impacts of a lack of fishery-dependent data involved the use of a recent stock assessment model for red porgy, a forward-projecting age-structured model developed during the Southeast Data, Assessment, and Review (SEDAR) stock assessment workshop. The model was an expansion of the Methot (1989) stock-synthesis model and is similar in structure to models used in assessment of cobia (Williams, 2001). With the red porgy model, we simulated a population through time, applying annual fishing mortality, natural mortality, recruitment, and growth (SAFMC[3]) while attempting to statistically match the simulated population with observed data sources. The stock assessment model incorporated data from 1972 through 2001. These data included information from fishery-dependent sources (commercial hook-and-line, trawl, and trap fisheries, and recreational headboats, charter boats, and private boats) and the fishery-independent MARMAP survey. Data included annual values for total landings by fishery, length and age frequencies by gear, and indices of abundance for the headboat fishery and MARMAP survey. Additional parameters incorporated in the model included natural mortality rate (assumed to be constant over time), gear selectivity for both MARMAP and fishery data, growth (based on the von Bertalanffy growth equation), recruitment (based on a Beverton-Holt recruitment model), and fishing mortality (SAFMC[3]). This model was specified and programed by SEDAR workshop participants using AD Model Builder software (vers. 6.0.3, Otter Research, Sidney, B.C., Canada).

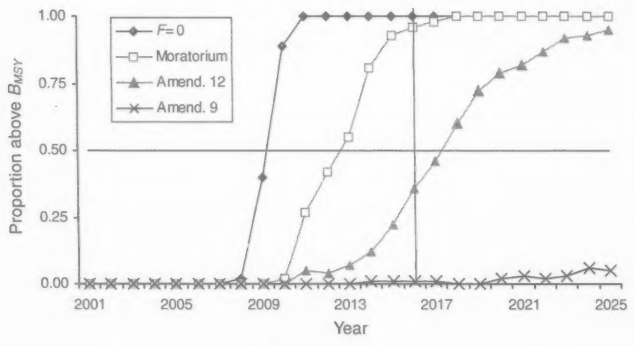

Figure 3

SEDAR population projections for red porgy (*Pagrus pagrus*) under four potential management scenarios. For a management option to be recommended, there must be at least a 50% likelihood (horizontal line) of the population biomass being greater than B_{MSY} before the year 2016 (vertical line).

Data modification

To simulate the lack of fishery-dependent information resulting from a moratorium, we omitted length- and age-frequency data used as input for the stock assessment model from commercial and headboat fisheries for the most recent 0, 1, 2, 3, 4, 5, or 6 years (Table 2). Landings, catch per unit of effort, life history parameters, and the model code were not altered. We did not remove landings from the stock assessment model because omitting landings would have changed the estimates of both fishing mortality and biomass, making comparisons of results among models impossible. Therefore, these simulations represent how the lack of fishery-dependent length and age information due to a moratorium would affect assessment results, rather than show the direct effects of reduced fishing mortality on the population. To incorporate stochasticity, we randomly sampled (with replacement) MARMAP length and age frequencies from observed frequencies. For each duration of moratorium (0, 1, 2, 3, 4, 5, and 6 years), we conducted 50 model runs. Results from the stock assessment models, including the status indicators relative biomass (B/B_{MSY}) and relative fishing mortality (F/F_{MSY}), were compared among simulations. In order to identify differences in variability, we calculated the standard deviation of status indicators among the 50 simulations for each simulated moratorium duration.

Population projections

Output from each of the stock assessment model runs was used as input for population projections to evaluate potential management options according to the method developed during the SEDAR process (SAFMC[3]). Starting with the biomass estimate from the most recent year (as estimated by each stock assessment model), stock projections were run under four potential management scenarios: 1) no fishing mortality or bycatch mortality, as if all fisheries in the region were closed (F=0); 2) fishing mortality under a red porgy moratorium (i.e. where there is only bycatch mortality [F=0.054]); 3) fishing mortality representative of Amendment 9 (F=0.173); and 4) fishing mortality representative of Amendment 12 (F=0.107; Table 1). SEDAR workshop attendees determined fishing mortality rate (F) for each option, and SEDAR projection results are shown in Figure 3 (SAFMC[3]).

The 25-year projections were based on a simulated age-structured population with stochastic stock-recruit relationship and fishing mortality. Initial (2001) stock size-at-age, weight-at-age, annual biomass and recruitment, B_{MSY}, and steepness estimated by the stock assessment model for each model run were used as input for population projections. Other projection input

that remained constant among model runs included natural mortality, maturity at age, and selectivity. Projections for each model run were repeated 100 times for each simulation. The resulting projections allowed us to investigate how data reduction would affect management decisions. For each moratorium length, we estimated the probability of rebuilding success as the proportion of the stochastic runs in which the biomass reached B_{MSY} before the rebuilding deadline of year 2016. For a management option to be recommended, the SAFMC wanted at least a 50% likelihood of the population biomass exceeding B_{MSY} before 2016.

Results

Variability among the simulations increased when multiple years of fishery-dependent length and age data were removed (Fig. 4, and Fig. 5, A and B). When only one or two years of fishery-dependent length and age data were removed, variability and status indicator estimates (such as B/B_{MSY} and F/F_{MSY}) did not differ substantially from simulations where no data were removed. However, when three to six years of fishery-dependent data were omitted, variability increased, especially for F/F_{MSY} (Figs. 4 and 5B). These trends in variability were also evident in population projections, where the range and confidence interval width of projected outcomes increased as data were removed (Fig. 6).

Additionally, removal of data led to higher estimates of population productivity (i.e., higher biomass and faster population rebuilding). When greater than three years of data were removed, projections tended to predict a slightly faster recovery (Figs. 6 and 7). Data availability would have affected management decisions for Amendment 12 because many data-poor models would have incorrectly identified Amendment 12 as a suitable management option (Figs. 6 and 7).

Discussion

Removing data from fishery-dependent sources for multiple years increased the variability of stock status indicators and projections. This variability was amplified during population projections, when the likelihood of rebuilding became increasingly variable as data were removed. Projections are, by nature, uncertain, but this uncertainty increased with even small reductions in information. Similar increases in variance were found by Chen et al. (2003) when information was removed from a New Zealand abalone (*Haliotic iris*) stock assessment model. When Chen et al. (2003) removed fishery-independent length data, standard deviation of parameter estimates increased 33%.

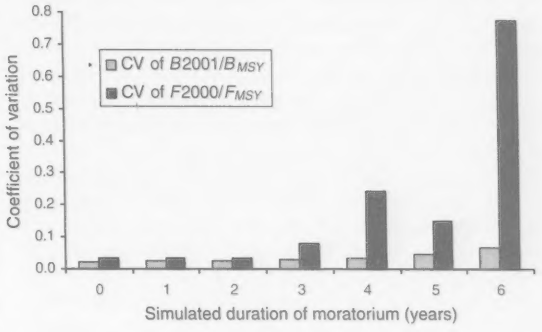

Figure 4

Coefficient of variation (standard deviation among 50 simulations for each moratorium duration divided by the mean) for red porgy (*Pagrus pagrus*) for B_{2001}/B_{MSY} and F_{2000}/F_{MSY}. Fishery-dependent length and age data were removed from the stock assessment model runs for the number of years specified.

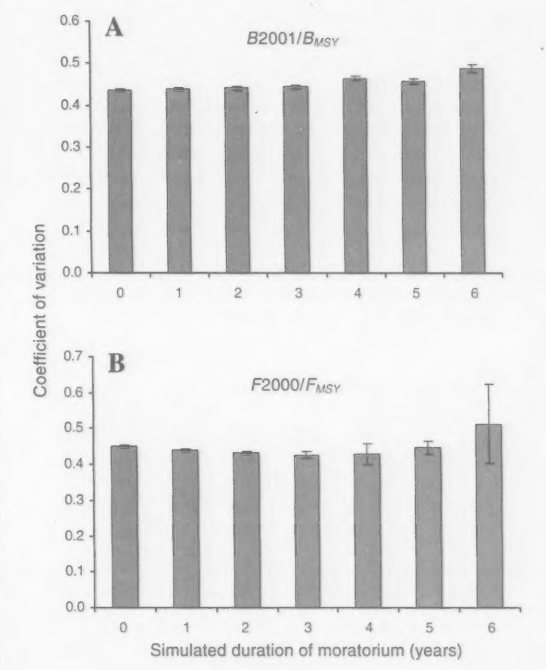

Figure 5

Mean estimates and 95% confidence intervals of (**A**) B_{2001}/B_{MSY} and (**B**) F_{2000}/F_{MSY} for 50 model runs for each moratorium duration for red porgy (*Pagrus pagrus*). Fishery-dependent length and age data were removed from stock assessment model runs for the number of years specified.

In addition to the expected outcome of higher variance as data were removed, we also found a slight tendency toward overestimating stock productivity that resulted from eliminating multiple years of data. When fishery-dependent length and age information were removed, the model tended to predict slightly higher biomass, lower fishing mortality, and faster population recovery. This finding was also supported by Chen et al. (2003), for whom data removal led to a more optimistic estimation of the current fishery status and stock productivity. This bias would increase the potential for overharvesting because the population may not be as productive as the model results suggest. The results of our study are specific to the South Atlantic red porgy stock and may not be applicable to other stocks or species. Stock status indicators and productivity estimates are affected by life history parameters, population size, historical and current fishing pressure, and data availability and these will differ among species. Additionally, use of an alternative stock assessment model could also affect results. However, if this bias is present for other species and stock assessment models, it could have serious implications for managers because it implies that the less information we have on a population, the more productive we would estimate (incorrectly) the population to be.

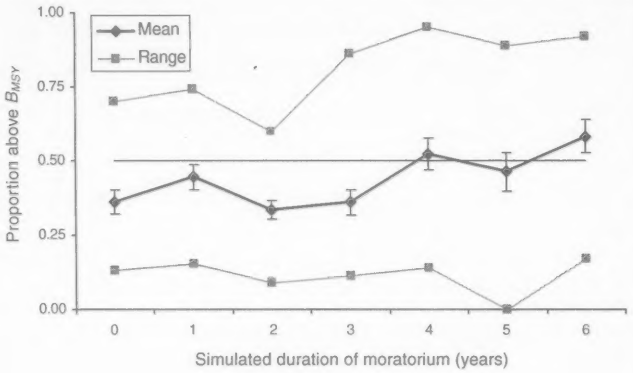

Figure 6

Proportion of projected red porgy *Pagrus pagrus* biomass estimates for the year 2016 under Amendment 12 for which the biomass was greater than B_{MSY}. The mean likelihood for 50 model runs for each moratorium duration is shown (with 95% confidence intervals) and the range of the 50 model runs is shown in gray. For a management option to be recommended, there must be at least a 50% likelihood (horizontal line) of the biomass being above B_{MSY}. Fishery-dependent length and age data were removed from stock assessment model runs for the number of years specified.

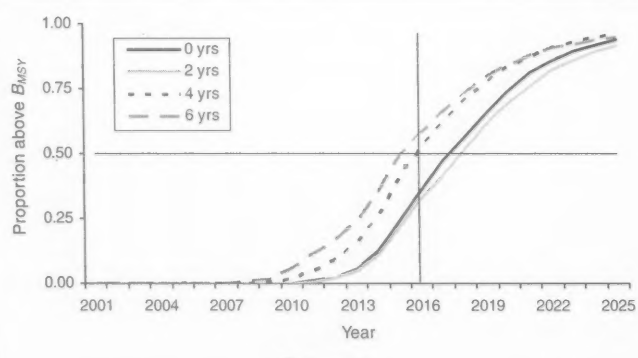

Figure 7

Stock projections (50 model runs for each moratorium duration) under Amendment 12 fishing mortality levels. Fishery-dependent length and age data were removed from stock assessment model runs for the number of years specified. For a management option to be recommended, there must be at least a 50% likelihood (horizontal line) of the population biomass being greater than B_{MSY} before the year 2016 (vertical line).

In general, removing red porgy length and age data had only minor effects on status indicator estimates, projections, or management decisions. The signal of a declining red porgy population was so strong and relatively consistent among data sources that removing a portion of this information did not greatly affect results. All model runs showed an overfished population but one that is not currently undergoing overfishing, and management decisions were also relatively consistent. In all cases, projections showed that rebuilding to B_{MSY} by the year 2016 would occur with no fishing mortality or a moratorium, and fishing mortality representative of Amendment 9 would be insufficient to rebuild the stock. Differences in management decisions did exist for model runs conducted under Amendment 12 fishing mortality levels; some data-poor models incorrectly identified Amendment 12 as a suitable option for rebuilding the stock. For a fish population closer to an overfished status or to a condition where overfishing is in progress, or where data sources were contradictory, data removal could affect stock assessment results and management decisions to a greater extent.

Because red porgy is a well-studied species for which there are 30 years of information from multiple sources, we removed a relatively small proportion of the data used in the stock assessment for our model runs. Conducting these types of simulations on a lesser-studied spe-

cies would most likely result in larger changes in status indicator estimates, projections, and management decisions because a larger proportion of information would be removed. The results of our study on red porgy identified the importance of investigating the potential effects of reducing fishery-dependent information on stock assessment results. If used before implementing management actions, this kind of data simulation study could estimate the potential impact of a lack of data before harvest restrictions are put in place that would cause data loss.

Management implications

These types of simulation studies aid in understanding the impacts of data quantity on stock assessments, particularly with respect to uncertainty and variance. By incorporating uncertainty due to data loss into management decisions, managers will be better able to assess and manage these populations. For example, SEDAR population projections estimated that red porgy required a 12-year moratorium for the population to rebuild to B_{MSY} (Fig. 3). However, our data simulations showed that variability surrounding status indicators increased when as few as three years of fishery-dependent data were removed (Fig. 4) and that a tendency toward overestimating productivity also increased with duration of the moratorium (Fig. 7). Therefore, if managers implemented a 12-year moratorium for red porgy (with no additional sampling), it is possible that a stock assessment conducted at the end of the moratorium would be unable to accurately estimate stock status and identify whether or not the population biomass had reached B_{MSY}.

This study highlights the importance of additional sampling during periods of strict regulations to compensate for the fishery-dependent data that are lost (Olney and Hoenig, 2001). Because many reef fish species are caught in the same fisheries, analysis of bycatch through a fisheries observer program would yield valuable data for a number of species. Another option for data collection would be to initiate a "test fishery" after a moratorium in order to collect fishery-dependent data in a relatively short time and then use these data to estimate stock status. A third option would be to use additional sampling during a moratorium from fishery-independent sources. Although MARMAP data are currently insufficient for assessments of many reef fishes, an expanded survey (i.e., into deeper water, more gear types, etc.) could prove to be valuable in future assessments. Even without a moratorium in place, assessments of many species would undoubtedly benefit from information collected by a fisheries observer program or an expanded fishery-independent survey. Data collected from these sources before a period of strict regulation would improve the ability of scientists to detect trends because a longer time series would make population recovery more apparent than that seen without such data.

The data quantity simulations conducted in our study could also be used for other species. This method allows managers to simulate the effects of a lack of data before enacting regulations or sampling changes that cause data loss. If a loss of information is shown to affect stock assessment results, simulations can be conducted to identify whether additional data will be needed and to test the effectiveness of additional sampling before implementing a sampling program. Stock assessments frequently use population projections to predict the effects of a policy on the stock. Our methodology is an expansion of this idea, using simulations to predict how a policy affects our ability to identify changes in the stock. By incorporating uncertainty due to data loss into management decisions, managers will be better able to assess and manage these populations and improve sampling to better fulfill future research needs.

Acknowledgments

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Habitat use of the inner continental shelf off southern New Jersey by summer-spawned bluefish (*Pomatomus saltatrix*)*

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Abstract—The goal of this study was to provide insight into habitat use of the inner continental shelf off southern New Jersey by summer-spawned bluefish (*Pomatomus saltatrix*). Throughout the August–October 1998 sampling period, a total of 1071 bluefish were collected from shelf surface waters, during which the mean density and body size was 3.7 bluefish/1000 m^3 and 13.7 mm standard length (SL), respectively. Spatiotemporal variability in bluefish density was explained by an inverse relationship with Secchi depth, and body size was explained by water temperature and depth. Bluefish size-structure in August was bimodal and comprised larval, transitional, and juvenile stages (3–48 mm SL). Size frequencies in subsequent months were unimodal and consisted of bluefish <25 mm SL. Synoptic sampling of multiple habitats indicated that the earliest life stages of bluefish extensively, and perhaps exclusively, use inner continental shelf surface waters. Summer-spawned bluefish numerically dominated the population across all habitats and temporal scales examined.

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Bluefish (*Pomatomus saltatrix*) is a coastal marine species that is common in temperate and subtropical waters worldwide (Juanes et al., 1996). Bluefish support extensive fisheries throughout their distribution (Juanes et al., 1996), including the western north Atlantic where this species has historically accounted for the greatest catch by weight in the recreational fishery (Pottern et al., 1989). Along the eastern coast of the United States, for example, bluefish landings in 1985 contributed to over 24% of the total marine recreational catch (U.S. Department of Commerce, 1986). Since the mid-1980s, however, bluefish landings in this area have declined precipitously and have yet to rebound in the last two decades (Klein-MacPhee, 2002). As a result, the Atlantic States Marine Fisheries Commission (ASMFC) established bluefish as a priority research subject and further recommended that research provide a better understanding of the early life history and recruitment patterns of this species.

Recruitment dynamics of bluefish along the eastern coast of the United States are intrinsically linked to annual spawning migrations of the adult population. Bluefish spawning migrations move northward into the Middle Atlantic Bight (MAB; Cape Hatteras, North Carolina, to Cape Cod, Massachusetts) during the spring and summer following an overwintering period in the South Atlantic Bight (SAB; Cape Canaveral, Florida to Cape Hatteras) (Klein-MacPhee, 2002) or at the edge of the continental shelf in the MAB (Miller, 1969; Wilk, 1982; Shepherd et al., in press). Pelagic eggs are spawned offshore during the spring and summer as bluefish migrate northward along the continental shelf. The planktonic eggs of bluefish experience a brief incubation period (48 hours; Deuel et al., 1966) that is followed by a larval stage that concludes 18–25 days after hatching and once the bluefish are 10–12 mm standard length (SL) (Hare and Cowen, 1994). Bluefish then undergo a transitional period, ending with the

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onset of the juvenile stage at 34–37 mm SL (Silverman, 1975). Juveniles remain oceanic for an additional 15–45 days before passively or actively recruiting to estuarine habitats at 40–80 mm fork length (FL) (Nyman and Conover, 1988; McBride and Conover, 1991; Hare and Cowen, 1993).

Along the U.S. northeastern coast, juvenile bluefish recruit to estuaries and have a consistent intra-annual and bimodal length-frequency distribution: the first cohort enters estuaries from late May to early June (spring-spawned cohort), and a second cohort enters from July to October (summer-spawned cohort) (Nyman and Conover, 1988; McBride and Conover, 1991; McBride et al., 1993; Creaser and Perkins, 1994). This is consistent with previous studies that indicate that juveniles of both spring and summer cohorts are estuarine dependent (Juanes et al., 1996; Able and Fahay, 1998). There is recent evidence, however, that select cohorts of bluefish may exclusively use alternative habitats, such as ocean beaches, during the juvenile stage (Able et al., 2003; Wilber et al., 2003). In addition, samples of larval and juvenile bluefish from surface waters on the inner continental shelf have indicated at least two cohorts of presumably summer-spawned fish that may not recruit to estuaries (Kendall and Walford, 1979; Rowe et al.[1]; Taylor and Able, in press).

Spring-spawned bluefish historically dominate juvenile year-class strength and were therefore assumed to determine adult population dynamics (Nyman and Conover, 1988; McBride and Conover, 1991; Munch and Conover, 2000). This assertion, however, is based primarily on estimates of juvenile abundance in MAB estuaries (Nyman and Conover, 1988; McBride and Conover, 1991) and failed to consider contributions from alternative habitats, including the inner continental shelf. A more recent evaluation of bluefish collected from the MAB also has indicated a shift in the cohort-specific production of juveniles over the last decade (Conover et al., 2003), such that summer-spawned fish numerically dominate recent year classes. Despite the apparent switch in the relative dominance of the two cohorts, bluefish successfully recruiting to the adult population remain the products of spring-spawning events (Chiarella and Conover, 1990; Conover et al., 2003). The factors underlying the apparent failure of the summer-spawned cohort to contribute substantially to the adult population are unknown. This failure is due, in part, to insufficient information that would otherwise enable a critical evaluation of each cohort's role in regulating year-class strength. Attempts to determine factors affecting recruitment patterns should include an evaluation of the cohort dynamics of summer-spawned bluefish that utilize inner continental shelf habitats.

The goal of our study was to provide greater insight into the habitat use by summer-spawned bluefish in a localized area in the MAB. In 1998, young-of-the-year (YOY) bluefish were sampled during the summer and fall on the inner continental shelf off southern New Jersey. Spatial and temporal abundance and distribution patterns were used to evaluate the potential importance of continental shelf waters as habitats for YOY bluefish. Observations from the 1998 study were then analyzed and compared to observations from other field surveys of habitat use by YOY bluefish in the same geographic region and time: inshore and other continental shelf waters of southern New Jersey in 1998 (Able et al., 2003).

Material and methods

Sampling of surface waters over the inner continental shelf

Bluefish were sampled at the water surface along the inner continental shelf off the southern coast of New Jersey (Fig. 1). Specifically, a 4×4 station grid (total area ~825 km^2) was sampled on ten dates between 11 August and 9 October 1998. Stations were grouped into four transects that were aligned parallel to the coastline (Fig. 1A). Transects closest and farthest from the coastline were 3 km and 18 km offshore, respectively. Water depths ranged between 6 and 29 m, and the shallowest depths generally occurred near the shore.

Bluefish were collected during daylight with a Methot trawl deployed at the surface (Methot, 1986; Oozeki et al., 2004). The frame trawl had a mouth area of 5 m^2, leading to an 11-m-long net (6-mm mesh) that tapered to a 2-m-long plankton net (0.5-m diameter, 500-μm mesh). One tow was performed at each of the 16 stations per sampling date, with the exception of 11 August and 9 October when only four and eight stations were sampled, respectively (n=140 total tows). At each station, the trawl was towed for four minutes in an arc (tow speed ~2.5–3.5 knots) to avoid the wake of the research vessel. All tows were made at the surface (0–2 m depth) with the top of the frame approximately 0.25 m out of the water. Samples were immediately processed after collection, and bluefish were preserved in 95% ethanol for subsequent laboratory analysis.

A General Oceanics flowmeter (General Oceanics, Inc., Miami, FL) was attached to the Methot trawl frame along a lower corner so that the volume of water sampled could be determined (~2000 m^3 per tow). Surface salinity, surface water temperature, water depth, Secchi depth, and wind speed and direction were recorded at all stations. Additional wind data were available as a time series (15-minute sampling interval) from a meteorological platform located at the Rutgers University Marine Field Station (Tuckerton, NJ; Fig. 1A; K. W. Able, unpubl. data).

[1] Rowe, P. M., K. W. Able, and M. J. Miller. 2002. Distribution, abundance, and size of young-of-the-year bluefish (*Pomatomus saltatrix*) in ocean and estuarine habitats in southern New Jersey during 1999–2000, 54 p. Jacques Cousteau Technical Report no. 100-16. Rutgers University, Institute of Marine and Coastal Sciences, Marine Field Station, 800 c/o 132 Great Bay Boulevard, Tuckerton, NJ 08087-2004.

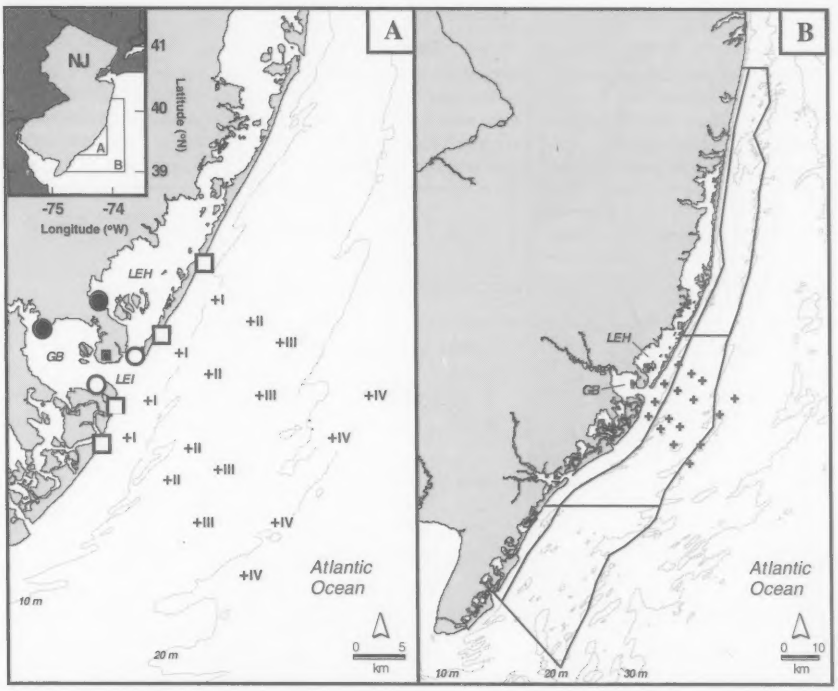

Figure 1

Map of inshore and inner continental shelf habitats off southern and central New Jersey. Plus symbols (✚) demarcate the 4×4 station grid (total area ~825 km^2) sampled with a surface-deployed Methot trawl on the inner continental shelf between 11 August and 9 October 1998. (**A**) Inner continental shelf sampling sites were grouped into four transects (I–IV) aligned parallel to the coastline. Estuarine (●), inlet (○), and ocean beach (□) sites sampled with a beach seine were located at the margins of Great Bay (GB), Little Egg Harbor (LEH), and Little Egg Inlet (LEI). (**B**) Solid lines (—) demarcate six depth strata sampled with an otter trawl on the inner continental shelf. Location of the Rutgers University Marine Field Station (Tuckerton, NJ; ■) and depth contours of 10, 20, and 30 m are provided.

Bluefish collected with Methot trawls were counted to estimate fish density (no. of bluefish/1000 m^3), measured to the nearest mm SL, and classified into distinct ontogenetic stages based on the individual's body size and presumed scale development (Silverman, 1975; Able and Lamonaca, in press). For the purposes of our investigation, several life history stages were demarcated: larval, transitional, and juvenile. The onset of scale development was recognized as the end of the larval stage and the beginning of the transitional period (12 mm SL; Silverman, 1975; Hare and Cowen, 1994). The transitional period in bluefish development, in turn, concluded with complete scale formation and the juvenile stage began at 34 mm SL (Silverman, 1975).

Spatial and temporal patterns of bluefish density and mean size were analyzed independently with multivariate repeated-measures analysis of variance (ANOVA) models by using station transects (transects I–IV; Fig. 1A) and sampling date (day of year) as the between-subject and within-subject factors, respectively. Profile transformation of the within-subject factor was used in the repeated-measures ANOVA model, and statistical significance was estimated from the Greenhouse-Geisser–adjusted probability to avoid violating the assumption of circularity (sphericity) of the within-subject variance-covariance matrix (von Ende, 1993). The mean density and body size of bluefish across four levels of transects and ten levels of sampling dates were contrasted with a Ryan-Einot-Gabriel-Welsch (Ryan's Q) multiple comparison test (Day and Quinn, 1989). Moreover, natural log (x+1) and natural log (x) transformations were performed on bluefish density and mean-size data, respectively, to meet assumptions of normality and homogeneity of variance. When data transformations did not achieve homoscedasticity, hypotheses were rejected at alpha values lower than the P-values of Levene's test for homogeneity of variance (Underwood, 1981).

The effects of several environmental parameters on the spatial and temporal distribution of bluefish density and mean size were analyzed with a stepwise multiple regression. The variables included in the regression

Table 1

Summary of field sampling protocols, habitat characteristics, and bluefish (*Pomatomus saltatrix*) catch and size data across multiple areas of southern and central New Jersey in the summer and fall of 1998. Bluefish catch data are reported as catch per unit of effort (CPUE). Temperature, salinity, and size data within parentheses represent minimum and maximum values observed on a given date, and NM and NA signify "no measurement" and "not applicable," respectively. Additional information regarding habitat location and sampling protocols is found in the text and Figure 1.

Habitat	Sampling gear	Sampling effort (no. of tows)	Depth (m)	Temperature (°C)	Salinity (‰)	CPUE (no. per tow)	Size (mm SL)
Continental shelf (surface waters)							
11–20 Aug 1998	Methot trawl	68	6–28	25.5 (16.5–27.3)	30.7 (30.0–31.1)	4.4	18.7 (3–48)
1–11 Sep 1998	"	32	6–29	24.0 (21.8–25.5)	30.6 (30.3–30.7)	2.3	10.1 (5–25)
18–25 Sep 1998	"	32	6–27	22.5 (21.0–23.6)	30.7 (30.3–31.0)	21.7	12.0 (4–24)
6 Oct 1998	"	8	9–29	19.5 (18.7–20.3)	30.7 (30.6–30.9)	0.6	18.7 (18–22)
Estuary							
13–24 Aug 1998	Beach seine	8	0–2	25.0 (24.0–26.0)	28.5 (28.0–29.0)	0.3	116.0 (60–172)
9 Sep 1998	"	5	"	19.9 (19.5–20.5)	28.0 (28.0–28.0)	0.4	111.0 (104–118)
21 Sep 1998	"	5	"	27.0 (27.0–27.0)	NM	0.2	116.0
5 Oct–3 Nov 1998	"	15	"	16.0 (10.5–19.0)	27.8 (26.0–29.0)	0.1	147.0
Inlet							
4–21 Aug 1998	Beach seine	9	0–2	25.7 (25.0–26.0)	29.3 (28.0–30.0)	3.3	83.1 (59–103)
3–4 Sep 1998	"	5	"	25.6 (25.0–26.0)	28.8 (28.0–30.0)	4.0	78.9 (55–113)
14–29 Sep 1998	"	10	"	21.7 (20.0–23.0)	29.7 (29.0–30.0)	0.5	96.2 (91–99)
13–29 Sep 1998	"	12	"	15.0 (13.0–17.0)	29.3 (29.0–30.0)	0.0	NA
Ocean beach							
3–25 Aug 1998	Beach seine	32	0–2	25.4 (23.0–27.0)	30.1 (28.0–31.0)	14.1	73.3 (51–168)
2–8 Sep 1998	"	16	"	24.4 (23.0–26.0)	30.4 (30.0–31.0)	53.7	76.5 (53–123)
14–30 Sep 1998	"	26	"	22.6 (20.0–26.0)	30.1 (29.5–31.0)	50.2	96.6 (27–205)
6 Oct–4 Nov 1998	"	41	"	15.6 (13.0–18.0)	30.0 (30.0–30.0)	93.2	118.5 (32–225)
Continental shelf (bottom)							
17–20 Aug 1998	Otter trawl	17	6-18	19.6 (12.3–25.4)	30.9 (28.3–31.5)	10.5	63.8 (30–200)
30 Oct–4 Nov 1998	"	17	"	14.4 (12.6–15.4)	31.4 (30.1–31.9)	21.6	125.6 (80–220)

model were sampling date (day of year), sampling time of day (sine-transformed), station distance from coastline (km), surface temperature (°C), surface salinity (‰), Secchi depth (m; a coefficient of light extinction or water clarity), water depth (m), and cross- and long-shelf wind speed (positive east and north, respectively). The significance level for entry into the regression model was set at $P<0.05$. Environmental variables that significantly affected the spatial and temporal distribution of bluefish density and mean size (i.e., those parameters incorporated into regression models) were also analyzed with an analysis of covariance (ANCOVA) model, with sampling date as the covariate and station transects as the discrete explanatory variable.

Synoptic analysis of habitat use by summer-spawned bluefish

Several other sampling programs initiated in 1998 monitored the distribution and size composition of YOY bluefish across multiple habitats in southern and central New Jersey (Table 1, Fig. 1) and the data from these programs were then compared to our data from surface waters on the inner continental shelf. A complete description of the sampling protocols and schedules for monitoring YOY bluefish in these habitats is provided elsewhere (Able et al., 2003; Rowe et al.[1]). Habitat use by different ontogenetic stages was ascertained from the size and stage (larval, transitional, juvenile) composition of bluefish observed in estuaries, inlets, ocean beaches, and the inner continental shelf. Accordingly, length-frequency histograms of bluefish were created for each habitat over four time periods (August, early to mid-September, mid-to-late September, and from October to November) by using class intervals of 5.0 mm SL for Methot trawl and beach seine samples, and 10.0 mm SL intervals for otter trawl samples. Moreover, a length-based key derived by McBride and Conover (1991) and adopted by others (Juanes and Conover, 1995; Wilber et al., 2003) was used to delineate between spring- and summer-spawned

bluefish in length-frequency histograms. Summer-spawned bluefish were defined as <100 mm SL in August, <125 mm SL from early to mid-September, <150 mm SL from mid-to-late September, <175 mm SL from October to November. Bluefish at body sizes larger then these groupings were designated as spring-spawned individuals.

Results

Bluefish density and mean size on the inner continental shelf

A total of 1071 bluefish were collected from surface waters off the southern coast of New Jersey during the survey. Throughout the August–October sampling period, bluefish were found in 71% of the tows (99 out of 140), during which the mean density was 3.7 bluefish/1000 m^3 (range=0–57.9 bluefish/1000 m^3). Bluefish density differed significantly by transect and sampling date (multivariate repeated-measures ANOVA; transect: $F=9.39$, df=3,12, $P<0.005$; date: $F=16.09$, df=9,88, $P<0.0001$). However, the transect-sampling date interaction effect was significant and precluded direct conclusions about the main effects (multivariate repeated-measures ANOVA; transect × date: $F=1.95$, df=27,88, $P<0.05$) (Fig. 2). The interaction effect was attributed to significantly higher densities of bluefish at transect II on days 226 and 268 (in comparison to transects I, IV, and transect I on these days, respectively (Ryan's Q multiple comparison test). Bluefish densities were also significantly greater at transect III on days 226 and 244 than at transect I for both dates (Ryan's Q multiple comparison test).

In the stepwise multiple regression, Secchi depth explained the most variability in bluefish density with an r^2 of 0.078 (stepwise multiple

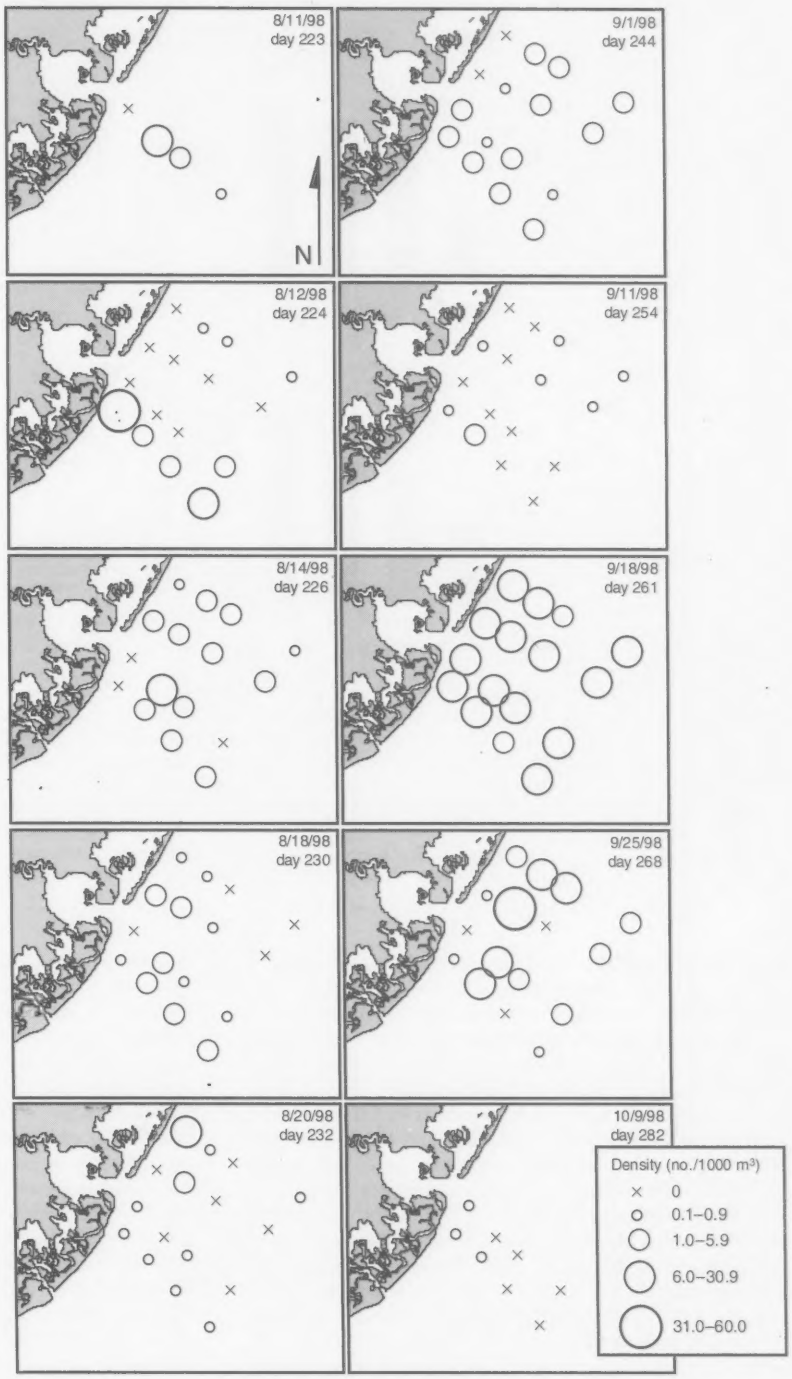

Figure 2

Spatial distribution of the density (no. of fish/1000 m^3) of bluefish (*Pomatomus saltatrix*) collected with a Methot trawl between 11 August and 9 October 1998 off the southern coast of New Jersey. Stations were located at approximately 39°27′N, 74°11′W.

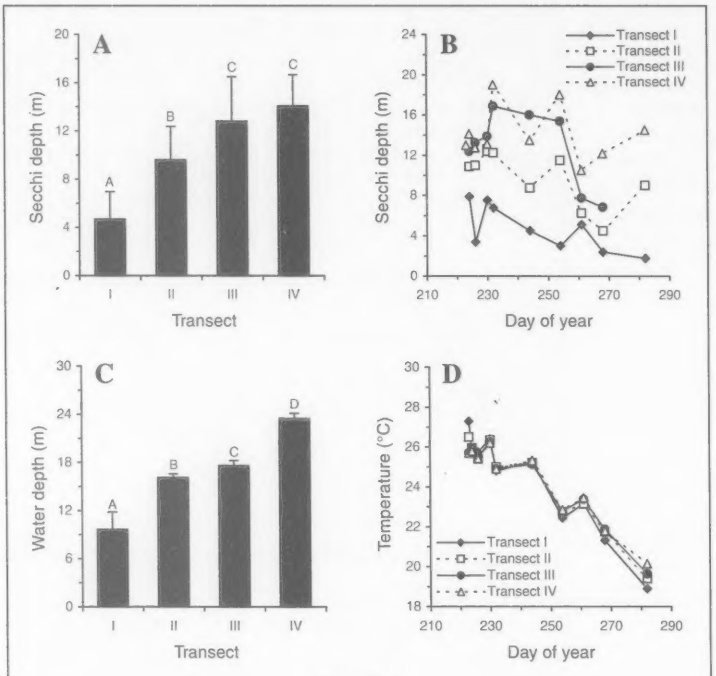

Figure 3

Spatial and temporal distribution (**A** and **B**) of Secchi depth (m), (**C**) water depth (m), and (**D**) surface water temperature (°C). Mean (±1 standard deviation) Secchi depth and water depth are displayed as a function of station transects (I–IV; Fig. 1A), calculated from ten sampling dates between 11 August and 9 October 1998 (days 223–282). Means with the same upper case letters are not significantly different (Ryan's Q multiple comparison test). Secchi depth and surface water temperature are also displayed as function of station transects and sampling date (days 223–224).

regression; F=11.34, df=1,135, P<0.001), and remaining parameters were not significant at P<0.05 and therefore not included in the model. The estimated coefficient for Secchi depth was negative (parameter estimate=–0.436), indicating an inverse relationship between bluefish density and water clarity. Before analyzing spatial and temporal variations in Secchi depths with an ANCOVA model, we examined the interaction effect between transect and sampling date. There was no significant transect-date interaction effect (two-way ANOVA; transect×date: F=2.47, df=3,124, P=0.065), and the assumption of equal slopes was met in the full data set (Underwood, 1981). Secchi depth differed significantly as a function of transect position (ANCOVA; F=63.34, df=3,127, P<0.0001), whereby distance from the coastline was positively correlated with Secchi depth (Fig. 3A). Furthermore, Secchi depth significantly decreased throughout the sampling period (ANCOVA; F=30.20, df=1,127, P<0.0001) (Fig. 3B).

The mean body size of bluefish collected from August to October was 13.7 mm SL (range=3–48 mm SL) (Table 1; Fig. 4). Similar to spatial and temporal density patterns, bluefish mean body size differed significantly by transect and sampling date (multivariate repeated-measures ANOVA; transect: F=6.16, df=3,12, P<0.01; date: F=7.50, df=9,50, P<0.0001) (Fig. 4). The transect-sampling date interaction effect was again significant (multivariate repeated-measures ANOVA; transect×date: F=3.50, df=24,50, P<0.0001), thereby precluding contrasts across main effects. The interaction effect was caused by significantly larger bluefish at transects I and II on day 254 compared to transects III, IV, and transect III, respectively (Ryan's Q multiple comparison test). On day 268, significantly larger bluefish were collected at transect IV than at all other transects (Ryan's Q multiple comparison test).

Surface water temperature and water depth were the most significant factors affecting the size distribution of bluefish (stepwise multiple regression; temperature: F=14.07, df=2,94, P<0.0005; depth: F=5.50, df=2,94, P< 0.05), such that temperature and depth accounted for a partial r^2 of 0.129 and 0.048, respectively (cumulative r^2=0.177). Moreover, estimated coefficients for both variables were negative (parameter estimates=–1.121

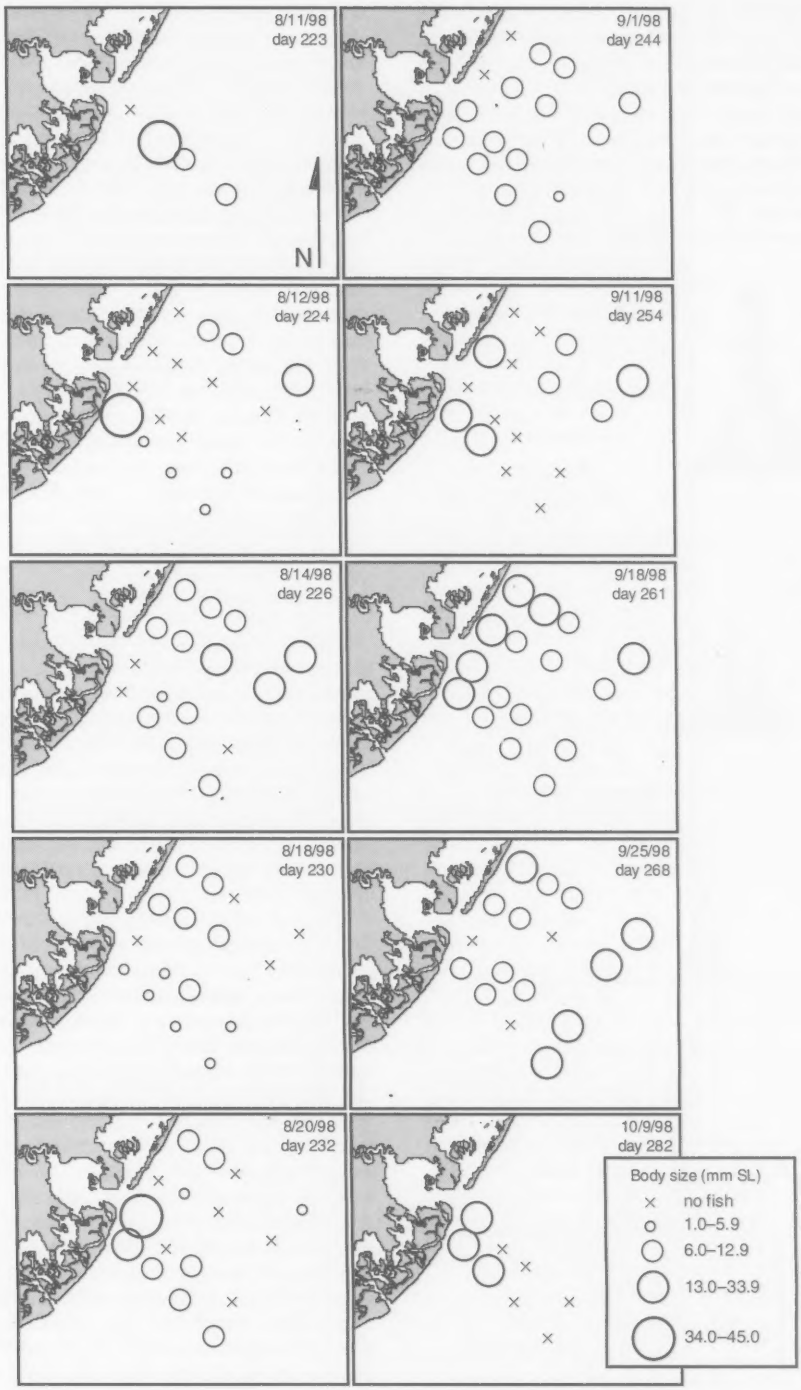

Figure 4

Spatial distribution of the mean size (mm SL) of bluefish (*Pomatomus saltatrix*) collected with a Methot trawl between 11 August and 9 October 1998 off the southern coast of New Jersey. Stations are located at approximately 39°27′N, 74°11′W.

and −0.254 for temperature and depth, respectively) indicating that larger bluefish were associated with relatively cool surface water and shallow water depths. Before analyzing spatial and temporal variations in temperature and depth with an ANCOVA model, we examined the transect-sampling date interaction effect. There were no significant interactions between transect and date for both analyses (two-way ANOVA; depth−transect×date: F=0.72, df= 3,132, P=0.5401: temperature−transect×date: F=1.87, df=3,132, P= 0.1385). Water depth significantly increased as distance from the coastline increased (ANCOVA; F=231.24, df=3,135, P<0.0001) (Fig. 3C), and surface temperature significantly decreased during the sampling period (ANCOVA; F=916.49, df=1,135, P<0.0001) (Fig. 3D).

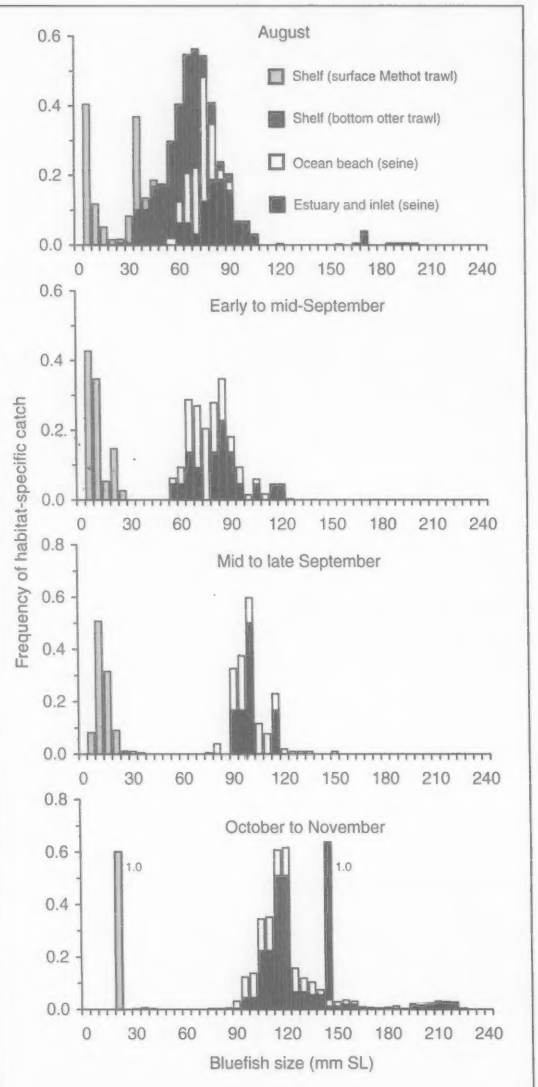

Figure 5

Composite length-frequency histograms for bluefish (*Pomatomus saltatrix*) collected from multiple habitats in summer and early fall (1998) in southern and central New Jersey. Additional information regarding habitat location and sampling protocols is found in the text, Table 1, and Figure 1.

Transitional bluefish (25–34 mm SL) and juveniles (35–50 mm SL) were a major portion of the overall size composition of bluefish collected in August (Fig. 5). For example, bluefish 25–50 mm SL constituted 40.1% of the individuals collected during this time period. In subsequent months, however, these bluefish were absent from remaining survey tows. Conversely, larval bluefish (3–11 mm SL) and small transitional bluefish (12–24 mm SL) were collected on all sampling dates and were numerically dominant in August and thereafter (Fig. 5). From August to late September, length-frequency distributions of bluefish <25 mm SL generally broadened in range and shifted to larger body sizes.

Synoptic analysis of habitat use by summer-spawned bluefish

Bluefish abundance and size-structure were compared among diverse inshore and coastal habitats in an effort to provide a more synoptic examination of summer habitat use across ontogenetic stages. In the process, bluefish were examined from shallow estuarine, inlet, and ocean beaches to surface and deeper waters on the inner continental shelf. As previously discussed, all individuals collected by Methot trawl tows from shelf surface waters were <50 mm SL, and therefore defined as summer-spawned larval, transitional, or juvenile bluefish (Fig. 5).

Bluefish catches in the Great Bay estuary were low; 33 seine hauls collecting five bluefish from August to October (0.1–0.4 bluefish/haul) (Table 1). With the exception of one bluefish, all individuals in the estuary were designated as summer-spawned fish (Fig. 5). Relatively few bluefish were collected in seine hauls at inlet sites located at the margin of Little Egg Inlet (55 bluefish from 36 hauls) that were primarily summer-spawned (Table 1; Fig. 5). In contrast to estuarine and inlet sites, substantial numbers of bluefish were collected from August to early November along ocean beaches north and south of Little Egg Inlet (6440 bluefish from 115 hauls) (Table 1). Spring-spawned bluefish were consistently collected along ocean beaches during the survey, but abundances were low compared to those of summer-spawned individuals that represented 98.4% of the total catch (Fig. 5). Compared to the sizes of bluefish collected from surface waters of the inner continental shelf, the sizes of the overwhelming majority (99.4%) of fish collected at inshore sites (estuary, inlet, and ocean beaches) were >50 mm SL (i.e., the sizes of juvenile fish). The only exception to this pattern occurred along ocean beaches from mid-September to early November (Fig. 5).

Sampling of bottom waters on the inner continental shelf during the same time period collected 179 and 367 bluefish in August and October–November, respectively (Table 1; Fig. 5). The size composition of bluefish collected from otter trawl tows was comparable to that observed at inshore sites (particularly ocean beaches), but distinctly different from that of fish captured in continental shelf surface waters. For example, 96.5% of the bluefish captured during sampling of shelf bottom waters were >50 mm SL (mean size=63.8 and 125.6 mm SL in August and October–November, respectively). Of the remaining individuals that were <50 mm SL, all were collected during the August otter trawl survey. Spring-spawned bluefish were collected in August and October–November by otter trawl tows, but again these bluefish represented a small portion of the total sampled population (5.1%).

Discussion

In our study, summer-spawned larval, transitional, and juvenile bluefish used the inner continental shelf extensively and represented a major portion of the entire fish assemblage collected in surface waters off the southern coast of New Jersey. For example, summer-spawned bluefish were the most frequently encountered species within the surface fish assemblage and ranked fourth in numerical dominance during the summer and early fall. Moreover, patterns of bluefish density observed in this study are consistent with those seen in other ichthyoplankton surveys in the MAB. Kendall and Walford (1979) found that bluefish larvae <4 mm SL were widely distributed in the MAB in August (Long Island, New York, to Virginia) and that peak concentrations occurred on the inner continental shelf in the vicinity of New Jersey and Delaware. Similarly, Smith et al. (1994) observed high densities of bluefish eggs in June and July and that centers of abundance occurred in mid-shelf waters off Delaware Bay and New Jersey (Berrien and Sibunka, 1999). Subsequent months were characterized by relatively broad spatial distributions of bluefish larvae from the central MAB to southern New England and by dense concentrations off New Jersey in July and August, followed by decreased abundance over the entire continental shelf in October (Kendall and Walford, 1979; Smith et al., 1994). These observations from the inner continental shelf, in conjunction with the reported use of inshore habitats by summer-spawned juveniles (McBride and Conover, 1991; Able et al., 2003; Wilber et al., 2003), indicate that coastal regions of New Jersey and adjacent areas are important summer-spawning sites for bluefish and, moreover, represent an appropriate location for synoptic comparisons of bluefish abundance and size-structure across habitats.

Empirical observations indicate that summer-spawned bluefish may use inner continental shelf habitats and, to a lesser extent, ocean beaches during their earliest life history stages (larval, transitional, and small juveniles). As surmised from this and previous studies, bluefish <50 mm SL are prominent constituents of the ichthyoplankton assemblage in the MAB (Kendall and Walford, 1979; Hare et al., 2001), but the these life stages are found rarely in estuaries and inlets. Field collections from our study indicated an abundant supply of larval to small juvenile bluefish in the vicinity of Little Egg Inlet from August to October, yet these particular life stages were not observed during concurrent sampling at estuarine sites. Moreover, larval fish assemblages were monitored over 16 years (1989–2004) inside Little Egg Inlet (Fig. 1), and bluefish were found in only 0.8% of the total 640 plankton tows performed between July and September (25 total bluefish, size range: 7.6–57.0 mm SL) (Witting et al., 1999; K. W. Able, unpubl. data).

In another study, juvenile bluefish were conspicuous members of the pelagic fish assemblage in Great Bay (Fig. 1), ranking fifth in frequency of occurrence and tenth in numerical dominance (Hagan and Able, 2003). The mean body size of bluefish collected in Great Bay, however, was 87.4 mm FL—a size that indicates that bluefish may not use estuaries during the earliest life history stages. More likely, YOY bluefish recruit to estuarine and ocean beach habitats as small juveniles (40–80 mm FL), as has previously been reported (McBride and Conover, 1991; Hare and Cowen, 1993; Able et al., 2003). This assertion was reconfirmed in our study by the synoptic examination of summer-spawned bluefish across multiple habitats, where the smallest bluefish collected in estuarine, inlet, and ocean beaches averaged 47.3 mm SL.

In contrast to the size-composition of bluefish inhabiting estuarine and coastal ocean sites, bluefish in surface waters on the inner continental shelf were strictly larval, transitional, and small juveniles <50 mm SL (Fig. 5). The paucity of juvenile bluefish >50 mm SL off the southern coast of New Jersey may be attributed to several factors including gear avoidance, size-dependent depth and habitat distributions, and active or passive emigration. First, gear avoidance appears unlikely because of the speed (~2.5–3.5 knots), duration (4 minutes), and frequency (140 tows) at which tows were performed (Norcross et al., 1974). For example, the approximate swimming speed of a 50-mm bluefish is 10 cm/s (Olla et al., 1985; Hare and Cowen, 1993) under the assumption that the fish swims at 2 body length/s (Hunter, 1981). At this rate, it is improbable that juvenile bluefish could actively avoid a Methot trawl being towed at 128–180 cm/s (1 knot=51.44 cm/s). Secondly, larval-to-juvenile bluefish are surface oriented (0–6 m), as indicated by collection efforts across different water depths (Norcross et al., 1974; Kendall and Walford, 1979; Kendall and Naplin, 1981; Shima, 1989) and by morphometric characteristics (e.g., silver and dark blue counter-coloration) of pelagic juveniles that indicate that they are adapted for a surface oceanic existence. Sampling in our study, however, was limited to the immediate surface layer (0–2 m), and therefore the current sampling design would not detect size-dependent depth distributions >2 m. In Virginian coastal

waters, Norcross et al. (1974) did not collect bluefish >22 mm total length in near-surface waters and attributed the absence of this fish to a lack of samples at depths where larger bluefish were presumably concentrated. In our study, continental shelf bottom waters were sampled with otter trawls (trawl vertical opening ~2 m), and the size of first occurrence was 30 mm SL. This finding indicates that juveniles may seek deeper water as body size increases and swimming ability improves (Norcross et al., 1974). Alternatively, small bluefish collected with otter trawl tows may have been concentrated in surface waters and were incidentally captured during initial gear deployment and final retrieval (i.e., under conditions when the otter trawl was inadvertently fishing the upper water column). Third, recruitment of juvenile bluefish >50 mm SL to estuarine or coastal habitats is another plausible explanation for their absence in continental shelf waters. As previously mentioned, bluefish actively or passively migrate inshore at 40–80 mm FL (McBride and Conover, 1991; Able et al., 2003). The size at which bluefish enter inshore habitats may be the result of biological timing and morphological constraints. These two factors are consistent with the fact that inshore recruitment co-occurs with a switch in diet from copepods to available piscine prey (Marks and Conover, 1993; Juanes and Conover, 1995). Correspondingly, bluefish may not enter estuaries until swimming ability improves and morphological development is complete, i.e., when fin ray development and scale formation (between 34 and 37 mm SL) are complete (Silverman, 1975). Swimming ability in many fish species dramatically improves after the transformation from larval to juvenile stages (Hunter, 1981; Stobutzki and Bellwood, 1994). If morphological development is coupled with improved swimming ability in bluefish, juveniles most likely have the physical ability to actively recruit to estuarine habitats from inner continental shelf waters (Shima, 1989; Hare and Cowen, 1993, 1996). This study provides cursory evidence that summer-spawned juveniles move inshore during August and early September. Furthermore, the disappearance of bluefish of 25–50 mm SL from continental shelf surface waters coincided with the appearance of somewhat larger fish (~50–60 mm SL) at estuarine and coastal ocean sites in late August and early September.

Along the northeastern coast of the United States (Cape May, New Jersey, to Long Island, New York), ingress of juvenile bluefish to inshore habitats presumably occurs as two distinct episodes (McBride and Conover, 1991 and references therein); which are consistent with intra-annual and bimodal length-frequency distributions. This bimodality in bluefish size-composition is a result of a first cohort recruiting inshore from late May to early June (spring-spawned cohort), and a second cohort entering the same geographic region from July to October (summer-spawned cohort) (Nyman and Conover, 1988; McBride and Conover, 1991; McBride et al., 1993). In our study, the size-composition of bluefish across habitats was multimodal, yet length-based information indicated that the overwhelming majority of YOY bluefish had been summer-spawned. Similarly, recent investigations of the inshore and continental shelf regions of the MAB also documented the numerical dominance of summer-spawned bluefish in late summer and early fall (Able et al., 2003; Conover et al., 2003; Wilber et al., 2003).

Although summer-spawned bluefish presumedly dominated the catches of YOY across all habitats and temporal scales examined in our study, the recruitment success and contribution of these cohorts to year-class strength is unknown. The abundance of these fish, compared to that of spring-spawned individuals, implies that they potentially make important contributions to bluefish year-class strength (Able et al., 2003); yet it is unknown whether the area sampled in this survey is indicative of bluefish abundance along other portions of the U.S. northeastern coast or whether this survey is representative of other years. Moreover, bluefish spawned later in the season (e.g., those encountered on the shelf in late September and October) may not achieve a size permitting either movement into estuaries or successful seasonal migrations. These bluefish, along with relatively small juveniles, may fail to contribute to the adult population because of size-selective mortality and decreased survival during overwintering periods (Hare and Cowen, 1997; Sogard, 1997; Hales and Able, 2001). There is also a consensus that spring-spawned juveniles frequently dominate the emigrating population in the fall, and therefore, are the key contributors to year-class strength (Nyman and Conover, 1988; Chiarella and Conover, 1990; Munch and Conover, 2000). This assertion has been recently contested, however, because other studies have indicated that summer-spawned bluefish contribute equally, if not exceedingly, to the YOY population (Able et al., 2003; Conover et al., 2003; Wilber et al., 2003). It is probable that bluefish population dynamics along the coastal United States are a function of the combined recruitment success of spring- and summer-spawned cohorts and that contributions vary annually or over decadal scales (McBride and Conover, 1991; Munch and Conover, 2000). As a result, future research must focus on broad geographical areas over sufficiently long temporal periods in order to adequately resolve the contribution of the different bluefish cohorts.

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Seasonal and size-based predation on two species of squid by four fish predators on the Northwest Atlantic continental shelf

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Abstract—Longfin inshore (*Loligo pealeii*) and northern shortfin (*Illex illecebrosus*) squids are considered important prey species in the Northwest Atlantic shelf ecosystem. The diets of four major squid predators, bluefish (*Pomatomus saltatrix*), goosefish (*Lophius americanus*), silver hake (*Merluccius bilinearis*), and summer flounder (*Paralichthys dentatus*), were examined for seasonal and size-based changes in feeding habits. Summer and winter, two time periods largely absent from previous evaluations, were found to be the most important seasons for predation on squid, and are also the periods when the majority of squid are landed by the regional fishery. Bluefish >450 mm, silver hake >300 mm, and summer flounder >400 mm were all found to be significant predators of squid. These same size fish correspond to age classes currently targeted for biomass expansion by management committees. This study highlights the importance of understanding how squid and predator interactions vary temporally and with changes in community structure and stresses the need for multispecies management in the Northwest Atlantic.

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Global depletion of marine predators has had dramatic effects on ecosystem structure and function (May et al., 1979; Jackson et al., 2001; Pauly et al., 2002). In many systems, the ramifications of such changes may not be fully realized. Groundfish declines have been linked to simultaneous increases in cephalopod landings in fifteen key Food and Agriculture Organization of the United Nations (FAO) areas (Caddy and Rodhouse, 1998). It is uncertain whether cephalopod populations are experiencing increased growth due to a release from predation (Piatkowski et al., 2001), or whether increased harvests are representative of the trend toward fishing species at lower trophic levels (Pauly et al., 1998). In the Northwest Atlantic, while gadids, flatfish, and other demersal species have been reduced because of overfishing (Link and Garrison, 2002), squid have risen in status from a mere bait fishery to one of the most economically important stocks in the region (Cadrin and Hatfield[1]).

Cephalopods have been documented as principal prey for numerous species of finfish, elasmobranchs, and marine mammals (Smale, 1996); however, in comparison to the ecological relationships between fish and their predators, less is known about the ecological interactions between squid and their predators. In a comprehensive evaluation of the Northwest Atlantic food web, bluefish (*Pomatomus saltatrix*), goosefish (*Lophius americanus*), silver hake (*Merluccius bilinearis*), and summer flounder (*Paralichthys dentatus*) were ranked among the most significant predators of squid (Bowman et al., 2000). Squid represented between 17% and 95% of the total mass consumed by these four finfish regionally. Dramatic changes in stock abundance and population structure have occurred since specimens for Bowman et al.'s study were collected 25–45 years ago. Exploitation of squid has risen substantially, and the four noted predators have experienced severe depletions; stock biomass levels have fallen as low as 20–50% of their respective maximum sustainable yield (B_{MSY}) limits (NOAA[2]). Additionally, the size structure of predator populations within the community has become skewed because of age-truncation. Recent evaluations of bluefish (Buckel et al., 1999a), goosefish (Armstrong et al., 1996), silver hake (Bowman, 1984), and summer flounder (Link et al., 2002) foraging habits have been conducted; however, sampling has been restricted to one or two seasons, primarily spring and fall. Analyses that base their results on feeding habits collected during a single season (Buckel et al., 1999b), or where results are based on data that have been pooled under the as-

[1] Cadrin, S. X., and E. M. C. Hatfield. 1999. Stock assessment of inshore longfin squid *Loligo pealeii*. Northeast Fish. Sci. Cent. Ref. Doc. 99-12, 107 p.

[2] NOAA (National Oceanic and Atmospheric Administration). 2001. Northeast Fisheries Science Center (NEFSC). Status of fishery resources off the northeastern United States. Website: http://www.nefsc.noaa.gov/sos/spsyn/species.html [accessed on 8 March 2006].

sumption that the diets collected in one season are a proxy for another (Overholtz et al., 2000) could overlook key periods of predation and lead to an underestimation of the total predatory demand imposed on principal prey resources, such as squid.

The two primary squid species found in Northwest Atlantic waters, longfin inshore (*Loligo pealeii*) and northern shortfin (*Illex illecebrosus*), are both highly migratory, and their distribution on the shelf is temporally variable. Squid move between inshore (spring and summer) and offshore (fall and winter) environments seasonally (Macy and Brodziak, 2001). On a diurnal basis they move from demersal waters during the day to surface waters at night (Lange and Sissenwine, 1983). The degree of vertical movement made by squid is also known to vary seasonally. Activity is more pronounced during warmer months when the water column is stratified and is diminished during winter and spring when shelf waters are well mixed (Hatfield and Cadrin, 2002). Prey availability and distribution in the water column, water temperature, and other environmental factors are believed to influence diel migration patterns (Cargnelli et al., 1999). Seasonal changes in squid behavior and habitat use will also affect encounter rates with different predators in the demersal environment.

Knowledge of species interactions is imperative to understand population dynamics and to manage stock recovery (Murawski, 1991). The present study provides a current assessment of the reliance on squid populations in the Northwest Atlantic region by four major squid predators; bluefish, goosefish, silver hake, and summer flounder. For each predator, ontogenetic and seasonal variations in feeding patterns were evaluated. Additionally, squid abundance in the demersal environment was related to predator diets as a mechanism for diurnal and seasonal changes in predation.

Materials and methods

Estimating changes in the abundance of longfin inshore squid

Longfin and shortfin squid are regularly caught in National Marine Fisheries Service (NMFS) bottom trawl surveys. However, catches of shortfin squid were exceptionally low over 2002 and 2003 (the time period evaluated during the present study), possibly because of poor recruitment. Catch data used in subsequent calculations were provided by NMFS bottom-trawl surveys (NMFS[3,4,5,6,7,8]). Sufficient information was available for longfin squid only; consequently abundance estimates were limited to this species. Furthermore, abundance surveys were not conducted during the summer; therefore adequate information was not available to evaluate this season.

To compare changes in longfin squid abundance in the demersal environment at different times of day and between seasons, the relative masses of prerecruits (W_P) and recruits (W_R) present were estimated by using the equations

$$W_{P(\text{year, season, time of day})} = \sum_t \frac{W_t P_{t(\text{year, season, time of day})}}{f_{t(\text{season, time of day})}} \quad (1)$$

$$W_{R(\text{year, season, time of day})} = \sum_t \frac{W_t R_{t(\text{year, season, time of day})}}{f_{t(\text{season, time of day})}} \quad (2)$$

where t = the index of tows made at NMFS stations in New York, New Jersey, Connecticut, Rhode Island, and Massachusetts respective to each year (2002, 2003), season (winter, spring, fall), and time of day (day, night, dawn and dusk);

W_t = the total mass of longfin squid caught in each tow; and

P and R = $(1 - P)$ estimate the proportion of biomass in each of two size classes, prerecruits (≤80 mm) and recruits (>80 mm), of longfin squid during each season.

f_t = the diel correction coefficient representing relative catch rates of longfin squid for each size class, season, and time of day as determined by Hatfield and Cadrin (2002) and was standardized to 1.0 during daytime for all seasons.

[3] NMFS (National Marine Fisheries Service). 2002. Fishermen's report: bottom trawl survey, Cape Hatteras–SE Georges Bank: February 5–March 2, 2002, FRV *Albatross IV*, 24 p. NMFS, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.

[4] NMFS (National Marine Fisheries Service). 2002. Fishermen's report: bottom trawl survey, Cape Hatteras–Gulf of Maine: March 5–April 25, 2002, FRV *Albatross IV*, 34 p. NMFS, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.

[5] NMFS (National Marine Fisheries Service). 2002. Fishermen's report: bottom trawl survey, Cape Hatteras–Gulf of Maine: September 4–October 25, 2002, FRV *Albatross IV*, 31 p. NMFS, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.

[6] NMFS (National Marine Fisheries Service). 2003. Resource survey report: bottom trawl survey, Cape Hatteras–Southern New England: February 4–March 1, 2003, FRV *Delaware II*, 19 p. NMFS, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.

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[8] NMFS (National Marine Fisheries Service). 2003. Resource survey report: bottom trawl survey, Cape Hatteras–Gulf of Maine: September 7–November 1, 2003, FRV *Albatross IV*, 35 p. NMFS, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA, 02543.

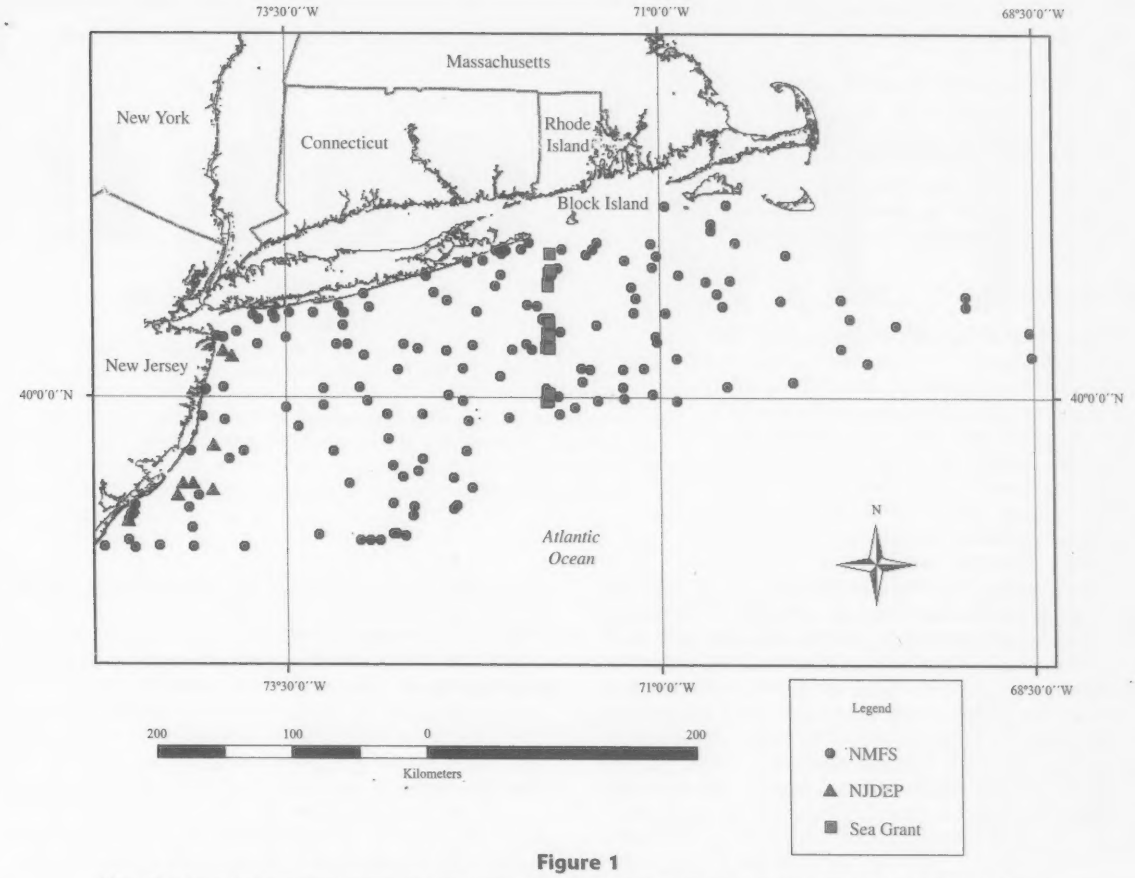

Figure 1

Map of fishery-independent sampling locations. Circles (●) are locations sampled during the National Marine Fisheries Service annual bottom-trawl survey cruise, triangles (▲) are locations sampled by the New Jersey Department of Environmental Protection, squares (■) are locations sampled during a Sea Grant sponsored cruise transecting the continental shelf along Block Island Sound Canyon.

To obtain an index of relative abundance, final mass values were divided by the number of tows made during each time of day, year, and seasonal period.

For Equations 1 and 2, values for P and R were estimated from longfin squid collected regionally during the winter, spring, and fall. Mantle lengths (mm) and the corresponding body weights (g) of individual squid measured in Hunsicker (2004) were used to calculate the percent distribution of biomass in each of the two size classes during each seasonal period. These estimated proportions were then used to partition the total catches reported at each NMFS station into prerecruit and recruit biomass. For each seasonal and diurnal period, catches were averaged between years and used to contrast relative concentrations of longfin squid in the demersal environment. Gear biases may affect the catchability of prerecruits more than recruits; therefore relative catch rates were compared among seasons only within each size class.

Sampling

Bluefish, goosefish, silver hake, and summer flounder were collected from continental shelf waters off the coasts of New York, New Jersey, Connecticut, Rhode Island, and Massachusetts from February 2002 to July 2003. Samples were obtained from two main sources: from fish landed by commercial fishing boats and from scientific survey cruises. Fishery-independent collections were made in conjunction with bottom trawl surveys conducted bimonthly by the New Jersey Department of Environmental Protection (NJDEP) and seasonally (except summer) by the National Marine Fisheries Service, Northeast Fisheries Science Center (NMFS-NEFSC) (Fig. 1). Samples were also collected aboard the RV *SeaWolf* (Sea Grant) during an independent survey that transected the continental shelf along the Block Island Sound Canyon (Fig. 1). The proportion of samples collected from fishery-independent sources is shown in

Figure 2 and the number of samples collected from all sources during all seasons is shown in Figure 3.

In addition to the stomach contents collected and analyzed for the present study, diet data collected regionally were drawn from the NMFS-NEFSC bottom trawl survey database. A full description of the survey design and collection methods used by the NEFSC can be found in Azarovitz et al.[9]

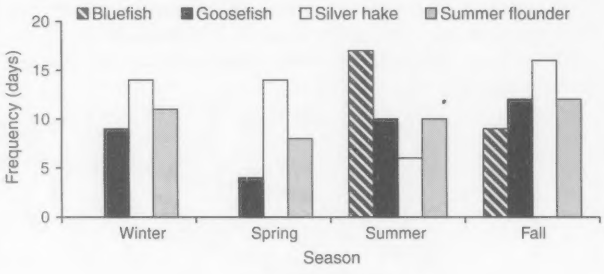

Figure 3

Frequencies (in days) of samples of bluefish (*Pomatomus saltatrix*), goosefish (*Lophius americanus*), silver hake (*Merluccius bilinearis*), and summer flounder (*Paralichthys dentatus*) collected from fishery-dependent and fishery-independent sources. No samples were collected for bluefish (*Pomatomus saltatrix*) during the winter and spring seasons.

Diet analysis

The majority of samples obtained from fishery-independent sources were processed onboard research vessels. However, only cursory assessments of prey type and mass could be made at sea; therefore samples were frozen and transported to the laboratory for a more thorough examination. Each fish was weighed and measured (fork length for bluefish, total length for goosefish, silver hake, and summer flounder), stomachs were removed, prey items were weighed to the nearest 0.01 gram and identified to the level of species whenever possible. With the aid of a dissecting microscope, otoliths, beaks, and other hard parts were recovered in order to classify species. When stomach contents could not be identified because of advanced stages of digestion, they were recorded as "unidentified animal remains." As with all diet studies, there is always a chance that a portion of samples are biased because fish may feed while in the net. This problem was addressed by excluding fish where prey was found (undigested) in the mouth and esophagus or where there was a clear difference in digestion stage among prey items found in the stomachs.

Three size classes, covering the total range of lengths of fish collected, were chosen for each species as follows: bluefish—small (200 to 450 mm fork length), medium (451 to 550 mm), and large (>551 mm); goosefish—small (50 to 250 mm total length), medium (251 to 450 mm), and large (>451 mm); silver hake—small (50 to 199 mm total length), medium (200 to 299 mm), and large (>300 mm); and summer flounder—small (250 to 399 mm total length), medium (400 to 549 mm), and large (>550 mm). Seasonal time periods were defined as winter (December–February), spring (March–May), summer (June–August), and fall (September–November).

[9] Azarovitz, T., S. Clark, L. Despres, and C. Byrne. 1997. The Northeast Fisheries Science Center bottom trawl survey program, 22 p. ICES Council Meeting 1997/Y:33.

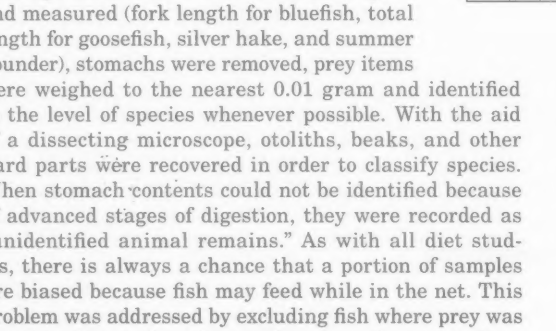

Figure 2

The proportion of samples of bluefish (*Pomatomus saltatrix*), goosefish (*Lophius americanus*), silver hake (*Merluccius bilinearis*), and summer flounder (*Paralichthys dentatus*) specimens collected from fishery-independent sources. No samples were collected for bluefish during the winter and spring seasons.

Statistical analyses

The Kruskal-Wallis test was used to test seasonal and size-based differences in predation on squid. A nonparametric test was chosen because of its robustness to assumptions of normality and skewness (Quinn and Keough, 2003). Preliminary analyses indicated that none of the data sets fitted the normal distribution and, owing to large numbers of zero values (representing the absence of squid in the diet), could not be transformed. Two sets of tests were performed on the data: first an "aggressive" set of tests were run by using individual fish as the sampling unit to give the maximum number of degrees of freedom; second, a "conservative" set of tests were run by using either stations (for data collected from fishery-independent sources) or cruises (for data collected from commercial fishery sources) as the sampling unit. The percent mass of squid in the diet of each fish (aggressive test) or pooled fish per station or cruise (conservative test) was determined and expressed as a propor-

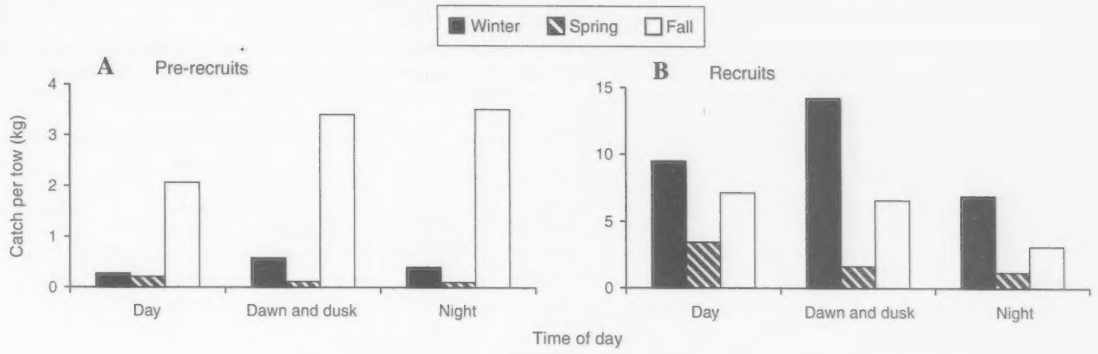

Figure 4

Relative catches of longfin inshore squid (*Loligo pealeii*) (**A**) prerecruits (≤80 mm mantle length) and (**B**) recruits (>80 mm mantle length) predicted in demersal waters during winter, spring, and fall of 2002 and 2003 (summer sampling was not conducted). Abundances of longfin inshore squid were measured as catch per tow (kg) and adjusted by seasonal diel correction coefficients specified in Hatfield and Cadrin (2002).

tion of the total mass consumed. To account for large numbers of tied rank values, an adjusted H test statistic was used to test the null hypothesis (Sokal and Rohlf, 1995). The two approaches produced similar results for the majority of tests. Therefore, only conservative test results are reported.

Results

Seasonal and diurnal differences in longfin inshore squid abundance

Predicted catches of longfin prerecruits during 2002 and 2003 indicated that the highest catch levels occured during the fall, intermediate levels during the winter, and minimum levels during the spring (Fig. 4A). These calculated values are similar to the historical abundance trends previously reported in Northwest Atlantic waters. Fall catches of prerecruits over all times of day were an order of magnitude higher in comparison to winter and spring values. The greatest variation in diurnal catches of prerecruits was predicted during the fall season (Fig. 4A). Conversely, catches of longfin recruits were estimated to be at their maximum during the winter, at intermediate levels during the fall, and at minimum levels during the spring (Fig. 4B). Maximum catch rates of longfin recruits were predicted during crepuscular and daytime periods of winter (Fig. 4B). Moreover, nighttime catches of recruits were two to three times higher during winter than during all other seasons.

Diet analysis

Bluefish Bluefish are present in Northern Atlantic waters only during the warmer months of the year; therefore sampling was restricted to the summer and fall seasons. A total of 299 bluefish from 26 sampling dates were analyzed. Fish ranged in size from 90 to 780 mm FL (average=469.6 mm). Overall, 53% of all bluefish sampled had food items present in their stomachs, and diets were split nearly equally between squid and fish. Perciforms were the dominant piscine prey; small amounts of amphipods and other pelagic crustaceans made up the remainder of the diet. A complete list of prey species recovered from all predator diets and their designated taxonomic groups can be found in Staudinger (2004).

Longfin squid was the primary squid species consumed by bluefish. A substantial amount of shortfin squid was also found in the stomachs of large fish (Table 1). Total predation on squid was greater during the summer than in the fall (Table 2); however, seasonal differences were not statistically significant possibly because of the high frequency of zero values in the dataset ($H_{adjusted}$=2.40, P=0.121, n=25). Medium and large fish were the primary consumers of squid, and small bluefish fed almost exclusively on fish (Table 1). Significant differences were found in the amount of squid consumed among all size classes of bluefish ($H_{adjusted}$= 6.62, P=0.037, n=75).

Goosefish A total of 536 goosefish stomachs were analyzed of which 269 (50%) contained prey. Goosefish ranged in size from 75 to 818 mm TL (average=341.1 mm). Goosefish were almost exclusively piscivorous; 93% of the total diet consisted of a mixture of gadiforms, clupeiforms, perciforms, and several other fish groups. Goosefish were the only species in the present study to prey on rajiforms.

Occurrence of squid in the goosefish diet was restricted to the winter and fall (Table 2) and differences among all seasons were significant ($H_{adjusted}$=15.27, P=0.002, n=46). Although medium size goosefish were

Table 1

Size-based stomach contents of fish collected in shelf waters of the Northwest Atlantic. Values presented are percentages of mass consumed (in grams). Fish lengths (small, medium, and large) are measured in millimeters. "Percent feeding" means the percentage of stomachs analyzed that contained prey. Bluefish were measured in fork length; goosefish, silverhake, and summer flounder were measured in total length.

	Bluefish			Goosefish		
Prey type	Small 200–450	Medium 451–550	Large 551+	Small 50–250	Medium 251–450	Large 451+
Squid	1.3	75.4	42.2	—	4.9	0.5
Longfin inshore squid	1.2	44.9	18.1	—	4.9	0.5
Northern shortfin squid	—	1.7	15.0	—	—	—
Unidentified squid	0.1	28.8	9.1	—	—	—
Fish	98.4	23.0	53.5	99.4	94.8	91.9
All other prey	0.3	1.6	4.3	0.56	0.24	7.68
Number of stomachs analyzed	103	99	113	148	153	235
Number containing prey (percent feeding)	76 (74)	51 (52)	49 (43)	96 (65)	75 (49)	98 (42)
Mean length (mm, SE)	316.6 (9.9)	509.8 (3.3)	628.6 (7.7)	124.8 (3.0)	358.2 (6.9)	540.0 (7.1)
Length range (mm)	200–438	460–547	555–780	75–241	255–450	460–818
	Silver hake			Summer flounder		
Prey type	Small 50–199	Medium 200–299	Large 300+	Small 250–399	Medium 400–549	Large 550+
Squid	0.0	2.7	18.6	16.7	33.5	20.6
Longfin inshore squid	0.0	2.7	12.3	15.3	25.4	14.7
Northern shortfin squid	—	—	0.2	—	—	5.3
Unidentified squid	—	0.1	6.1	1.4	8.1	0.6
Fish	34.7	17.6	62.0	67.2	55.1	76.0
All other prey	65.33	79.63	19.33	16.13	11.40	3.44
Number of stomachs analyzed	174	566	240	316	360	154
Number containing prey (percent feeding)	132 (76)	298 (53)	108 (45)	85 (27)	91 (25)	54 (35)
Mean length (mm, SE)	150.5 (3.1)	260.4 (1.5)	334.6 (3.9)	346.1 (4.4)	454.9 (4.1)	608.2 (6.4)
Length range (mm)	60–199	200–298	300–484	250–399	400–530	550–750

the only size class found to consume squid in notable amounts (Table 1), differences in the proportions of squid consumed among all size classes were not significant ($H_{adjusted}$=3.11, P=0.211, n=138). All squid found in the goosefish diet were classified as longfin squid.

Silver hake Of the 980 silver hake stomachs examined, over half (55%) contained prey. Silver hake ranged in size from 60 to 484 mm TL (average=248.3 mm). Feeding rates for silver hake were highest during the summer months and lowest during the spring and fall. Overall, silver hake fed primarily on fish and crustaceans, and lesser amounts of squid and other invertebrates. Amphipods and euphausiids were the dominant crustacean prey. Consumption of gadiforms, including conspecifics and unclassified osteichthyans, made up the majority of piscine prey.

Predation on squid differed significantly among seasons ($H_{adjusted}$=10.03, P=0.018, n=55) and was at its maximum during winter (Table 2). Silver hake diets exhibited a pronounced shift towards squid with increasing size (Table 1). Small and medium hake ate negligible amounts of squid. Conversely, squid totaled nearly 20% of all mass consumed by large hake. Differences in squid predation among size classes were significant ($H_{adjusted}$=7.58, P=0.023, n=132). Longfin squid was the dominant species of squid identified in the silver hake diet.

Summer flounder Of the 830 summer flounder analyzed, only 28% were found to be actively feeding. Summer flounder spend the juvenile stage of their life cycle in estuaries along the Northwest Atlantic coast; hence few flounder <280 mm were present in the analysis. Fish ranged in size from 250 to 750 mm TL (average=450.7 mm). Overall, diets consisted primarily of fish, squid, and stomatopods. Perciforms and clupeiforms were the dominant piscine prey.

Table 2

Seasonal stomach contents of fish collected in shelf waters of the Northwest Atlantic. Values presented are percentages of mass consumed (in grams). Fish lengths are measured in millimeters. No bluefish (*Pomatomus saltatrix*) were collected during the winter and spring seasons. "Percent feeding" means the percentage of stomachs analyzed that contained prey. Bluefish were measured in fork length; goosefish, silver hake, and summer flounder were measured in total length.

	Bluefish				Goosefish			
Prey type	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
Squid	—	—	58.2	10.7	2.9	—	—	3.9
Longfin inshore squid	—	—	31.7	3.2	2.9	—	—	3.9
Northern shortfin squid	—	—	7.2	7.5				
Unidentified squid	—	—	19.3	—				
Fish	—	—	38.7	88.6	83.7	100.0	96.5	96.0
All other prey	—	—	3.1	0.7	13.39	0.00	3.45	0.13
Number of stomachs analyzed	—	—	236	67	206	22	259	49
Number containing prey (percent feeding)	—	—	114 (48)	45 (67)	58 (28)	8 (36)	175 (68)	28 (57)
Mean length (mm, SE)	—	—	495.0 (12.4)	405.9 (24.6)	462.1 (16.3)	523.8 (26.2)	273.4 (13.4)	462.1 (25.4)
Length range (mm)	—	—	230–737	90–780	160–780	420–620	75–818	170–690

	Silver hake				Summer flounder			
Prey type	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
Squid	15.6	1.6	0.0	0.7	49.0	0.5	22.1	12.4
Longfin inshore squid	11.4	0.3	0.0	0.6	41.2	0.5	5.2	8.6
Northern shortfin squid	—	0.4	0.0	—	7.6	—	—	—
Unidentified squid	4.1	1.0	—	0.1	0.2	—	16.9	3.9
Fish	30.3	35.7	34.6	65.4	49.6	99.5	37.9	81.8
All other prey	54.1	62.7	65.3	33.8	1.40	0.04	39.93	5.76
Number of stomachs analyzed	308	365	165	143	407	103	120	196
Number containing prey (percent feeding)	163 (53)	165 (45)	146 (88)	64 (45)	77 (19)	22 (21)	65 (54)	66 (34)
Mean length (mm, SE)	270.7 (4.7)	262.8 (5.7)	198.5 (4.8)	268.0 (6.9)	477.5 (12.6)	446.9 (30.1)	431.2 (11.1)	439.7 (12.9)
Length range (mm)	60–484	79–480	103–410	110–450	270–710	300–750	268–645	250–690

The proportion of squid consumed by summer flounder fluctuated significantly among seasons ($H_{adjusted}$=14.29, P=0.003, n=43). Predation on squid was at its maximum during winter, and elevated during the summer in comparison to spring and fall (Table 2). Although differences in squid predation among size classes were not significant ($H_{adjusted}$=2.33, P=0.312, n=132), squid contributed the greatest relative amount to the diet of medium flounder (Table 1). The dominant species of squid identified in all size classes and for all seasons was longfin squid. Shortfin squid was found only in the diets of large flounder (Table 1) and only during the winter season (Table 2).

Discussion

Seasonal predation on squid

Previous descriptions of predation on squid in the Northwest Atlantic have been based on sampling in the fall and, to a lesser extent, during the spring seasons. Survey

cruises conducted by the NMFS during these two periods were the primary data source for these prior analyses. The present study indicates that these two seasons are not wholly representative of total predation pressure on squid; indeed, winter and summer may be primary periods for predation on squid. Consequently, previous estimates of the total predatory demand imposed on squid populations by these predators may have been underestimated (Buckel et al., 1999b; Overholtz et al., 2000). It should be noted that in order to collect adequate numbers of fish during all four seasons, fishery-dependent sources were used. However, nonrandom sampling could have influenced seasonal differences seen in the present study.

It is likely that heightened predation on squid during the winter season reflects an increase in habitat overlap by both predator and prey. All species of squid and fish evaluated in this study are known to retreat to warmer waters of the outer shelf and slope during the colder months of the year. This movement may act to concentrate fish and squid and lead to elevated predator-prey encounter rates. Predicted nighttime and crepuscular catches during winter indicate that longfin squid are at higher concentrations in the demersal environment than at other seasons and reflect diminished vertical migrations by squid (Hatfield and Cadrin, 2002). Increased residence time in bottom waters may make squid more susceptible to demersal predators and may explain their marked increase in silver hake and summer flounder diets during winter. Although the present study has made contributions to increase knowledge of predation rates during summer, data on squid abundance levels were insufficient to make inferences about predator interactions during this season.

Historically, longfin squid seasonal biomass on the shelf has been estimated to be at its maximum during the fall (Cargneli et al., 1999). This trend was reflected in catch results for prerecruits during the time period evaluated; however, this supposed increase in availability was not reflected in predator diets. Instead, summer flounder and bluefish both exhibited diminishing reliance on squid and increased predation on similar piscine prey (Staudinger, 2004). It is unclear whether predator and squid size relationships or predator preference is mediating bluefish and summer flounder foraging behavior; therefore further studies are warranted. Alternatively, it has been acknowledged that the NMFS fall bottom-trawl survey has better coverage of the shelf than the winter and spring surveys, as well as the greatest overlap with the distribution range of longfin squid.[10] Both of these factors could influence seasonal historical abundance estimates and inaccurately represent the fall population in relation to other times of year.

Size-based shifts in predation by fish

Ontogenetic shifts in feeding commonly take place in the early life stages of a fish. However, for many species, less is known about progressive shifts through the adult stages of growth (Gerking, 1994). Bluefish showed a dramatic shift in diet at lengths of approximately 450 mm, transitioning from a diet primarily of piscine prey to that of squid. Longfin squid was the dominant cephalopod identified in the diets across all sizes of bluefish; however, shortfin squid was found to increase in importance in large bluefish. It is at this larger (551+ mm) size that bluefish begin to inhabit outer-shelf and offshore waters (Fahay et al., 1999). Because shortfin squid are more pelagic than longfin squid (Brodziak and Hendrickson, 1999), this change in diet may reflect an ontogenetic shift towards offshore food resources as bluefish mature.

Silver hake also exhibited a strong and positive increase in predation on squid with increasing size. Significant differences were observed among size classes—the greatest amount of squid being consumed by fish 300 mm and greater. The size at which silver hake were found to begin feeding on squid is similar to that found in previous studies (Garrison and Link, 2000). However, the relative proportions consumed by large hake were found to be nearly double those previously reported. It is possible that the findings of the present study represent an expanded view of the silver hake diet at larger body sizes because of intensified sampling over all seasonal periods. Alternatively, increased squid consumption could reflect decadal differences in squid availability.

Summer flounder spend the juvenile stage of their lives in bays and estuaries. Link et al. (2002) reported squid in the diets of individuals smaller than those examined in the present study. Therefore, the initial shift toward squid by young flounder as they transition from inshore to offshore waters may not have been realized. In fish that were sampled on the continental shelf, squid were found to be an important constituent of diets across all body sizes. Although a statistically significant shift among size classes was not detected, predation on squid was observed to peak in medium-size fish. This finding is similar to that of Bowman et al. (2000), who determined squid consumption peaked between 500 and 600 mm and then declined again for larger fish.

Bowman et al. (2000) reported cephalopods as a major constituent (>20%) of the goosefish diet in the southern New England region. In a study conducted by Armstrong et al. (1996), longfin squid were found in small goosefish (<400 mm TL) stomachs during summer and represented approximately 10% of the diet. In contrast, the present study found that squid contributed trivial amounts to the diet of goosefish across all size classes and seasons. It is unclear why such vast discrepancies were observed between these studies. One possible ex-

[10] NEFSC (Northeast Fisheries Science Center). 2002. Report of the 34th northeast regional stock assessment workshop (34th SAW): stock assessment review committee (SARC) consensus summary of assessments. Northeast Fish. Sci. Cent. Ref. Doc. 02-06, 356 p. National Marine Fisheries Service, 166 Water St., Woods Hole, MA 02543.

planation is that the opportunistic foraging strategy of goosefish is more sensitive to variation in relative and overall abundances of prey and results in erratic food habits over various time scales.

Predator–prey behavior

Differences in the amount of squid consumed among species, among predator sizes, and seasonal periods indicate that aspects of predator and prey behavior must be playing a pivotal role in influencing the susceptibility of squid to predation. Seasonal inshore-offshore habitat use and diurnal vertical migrations are two mechanisms that may act to mediate predator-prey encounter rates. Other behaviors that influence encounter rates are the times of day that each predator is actively hunting and the areas of the water column being searched. Of the four predators evaluated, seasonal movements by summer flounder are most similar to the migration patterns of longfin squid. Summer flounder are primarily daytime feeders and spend the majority of their time on or near the seafloor (Packer et al., 1999). Conversely, silver hake are a demersal species known to be active hunters primarily in the late afternoon and evening (Bowman, 1984). Large vertical movements in the water column are not customary for silver hake (Bigelow and Schroeder, 1953), therefore nighttime feeding limits interactions during seasons when squid exhibit strong diurnal migrations. Bluefish are the only predator in this study considered to be pelagic and that actively pursue prey throughout the water column. Although bluefish have been shown to forage primarily during the day (Juanes and Conover, 1994), it is possible that there is a seasonal shift in depth at which bluefish forage (Bigelow and Schroeder, 1953). A shift from feeding at depth in the late spring and summer to feeding in the surface waters during fall may explain, in part, seasonal differences in importance of squid to bluefish because few (if any) squid are present in the upper water column during daylight.

In general, daytime foraging behavior, combined with positioning in the demersal environment, create the optimal setting for regular encounters between squid and fish predators and explain differences in the proportion or even presence of squid in the diet between species with similar geographical ranges.

Implications for management

Since the late 1980s, squid harvests have increased substantially during the winter. Offshore harvests have been, on average, three times greater than inshore catches between October and March (Cadrin[11]). The combination of increased fishing pressure and elevated predation rates concentrated within a single season may not be sustainable for a species, such as squid, with a life span of less than a year and that has little overlap between generations (Pierce and Guerra, 1994). If not properly accounted for, this increase in total mortality on squid during the winter could affect the number of squid surviving to spawn during spring and summer and limit available biomass for predators such as bluefish and summer flounder.

Another area of concern stems from potential increases in top-down pressure from recovering predator populations. Regionally, management has emphasized age-truncation of predators as one of the most serious factors affecting summer flounder and silver hake populations. The age classes of summer flounder (age-2) (Terceiro[12]) and silver hake (age-3) (Brodziak[13]) targeted for expansion in their respective management plans, correspond to the lengths and associated ages identified in the present study as being the most voracious predators of squid. If management objectives are met and summer flounder and silver hake stocks are fully rebuilt, predation on squid could rise substantially as fish that have been functionally absent from the population begin increasing in abundance.

Other species, such as bluefish, that have been severely overfished are also showing signs of recovery (ASMFC[14]). Consumption of squid by bluefish has been estimated to exceed the mass removed by the fishing industry (Buckel et al., 1999b) and is contingent on predator population abundance (Overholtz et al., 2000). If one includes summer foraging habits, total consumption of longfin squid by bluefish may be much greater than previously estimated. In light of this new information, a reassessment of the predatory demand imposed by bluefish and other recovering predators on squid is clearly needed before fish stocks are fully rebuilt.

The simultaneous exploitation of predators and their prey, when there is limited information about species interactions, is a precarious practice that can have unintended and potentially detrimental consequences for one or both stocks. Depletion of biomass that supports higher predators may decrease biological production. Conversely, prey populations may become overextended. A greater understanding of species relationships is necessary, especially in ecosystems where fishing occurs at multiple trophic levels. The present study shows that consideration of predation year-round and for a range of predator sizes is imperative to accurately assess

[11] Cadrin, S. X. 2001. Status of fishery resources off the northeastern United States: longfin inshore squid. Website: http://www.nefsc.noaa.gov/sos/spsyn/iv/lfsquid/ [accessed on 8 March 2006].

[12] Terceiro, M. 2003. Stock assessment of summer flounder for 2003. Northeast Fisheries Science Center Reference Document, 179 p. National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA, 02543.

[13] Brodziak, J. 2001. Status of fishery resources off the northeastern United States: silver hake. Website: http://www.nefsc.noaa.gov/sos/spsyn/pg/silverhake/ [accessed on 8 March 2006].

[14] (ASMFC) Atlantic States Marine Fisheries Commission. 2003. Website: http://www.asmfc.org [accessed on 8 March 2006].

predation pressure on squid populations. As predator populations in the Northwest Atlantic are recovered under current management initiatives, a multispecies management approach will be crucial to avoid conflicts between squid and finfish fisheries and should be applied to species beyond those presented in this article.

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Evidence for resource partitioning and competition in nursery estuaries by juvenile flatfish in Oregon and Washington

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Resource partitioning among co-occurring species can provide evidence that density-dependent survival can be a function of interspecific competition. Of the early life history stages of flatfish, the juvenile phase is thought to be the most susceptible to density-dependent mortality, and intraspecific competition among individuals is thought to lead to decreased survival of extremely strong year classes (Iles and Beverton, 2000). Juveniles of multiple flatfish species are often observed to coexist in a single nursery area (e.g., Burke et al., 1991; Henderson and Holmes, 1991; Reichert and van der Veer, 1991; Norcross et al., 1997), but evidence for interspecific competition is rarely examined. We examined evidence for resource partitioning and interspecific competition among juvenile flatfish species co-occurring in nursery areas.

Flatfish species often have juvenile nursery areas that are segregated from the adult population. In many cases, juveniles use shallow nearshore habitats as nursery areas, and adults are found in deeper offshore habitats (Gibson, 1994; van der Veer et al., 2000). On the Pacific coast of North America, estuaries are typically smaller and occur less frequently than in other areas such as the Atlantic coast of North America. Possibly because of the limited estuarine habitat on the West Coast, fewer species of marine fish and invertebrates use coastal estuaries for nursery areas. In our study, we examined the spatial distribution of co-occurring juvenile flatfish populations within Pacific coast estuaries. The four species examined were English sole (*Pleuronectes vetulus*), Pacific sanddab (*Citharichthys sordidus*), sand sole (*Psettichthys melanostictus*), and starry flounder (*Platichthys stellatus*). Juveniles of these species are found in Oregon and Washington estuaries during the summer, and adults of each of these species contribute to a lucrative trawl fishery on the coastal shelf.

To date, estuarine residency of juvenile English sole has been well documented (Krygier and Pearcy, 1986; Gunderson et al., 1990; Rooper et al., 2003); however, this is the first comparison of the spatial distribution of the three other species within estuaries, and is the first study to encompass such a wide region of coastal estuaries (ranging over 400 km of coastline). The goal of this study was to compare the summer distribution of juvenile English sole, starry flounder, sand sole, and Pacific sanddab within nursery estuaries over three years, to determine whether the four flatfish species were spatially partitioning the nurseries. We also examined the summer distribution in relation to the abundance of species across years and habitats in order to determine the potential for interspecific competition.

Materials and methods

Study area

This study was carried out at four estuaries on the Oregon and Washington coasts: Grays Harbor, Willapa Bay, Coos Bay, and Yaquina Bay (Fig. 1). Seventeen to 20 trawl sites were chosen within each estuary, and each trawl site was classified into three habitat types: lower main channel, lower side channel and upper estuary. Habitat delineations were previously identified by principle component and discriminant function analysis (Rooper et al., 2003). The lower estuarine sites were on average deeper (depth=5.1 m), colder (13.6°C), and more saline (28.5 ppt) than upper estuarine sites because of their proximity to the mouth of the estuary. On average, lower side channel sites were slightly warmer (15.6°C), shallower (depth=3.7 m) than the lower estuarine sites, and had extensive tide flats that surrounded the sites and were exposed during low tides. Upper estuarine sites were typically shallow (depth=4.0 m), very warm (17.0°C), less saline (25.1 ppt), and had a large sediment size and a smaller area of surrounding tidal flats (Rooper et al., 2003).

Sampling procedures

Trawl surveys of all four estuaries were conducted in both June and August from 1998 through 2000. In each month all four estuaries were sampled over two and a half weeks and a total of 431 trawl hauls were completed over the three summers. The same sites were resurveyed throughout all years of sampling; however the exact trawl location varied somewhat between sampling

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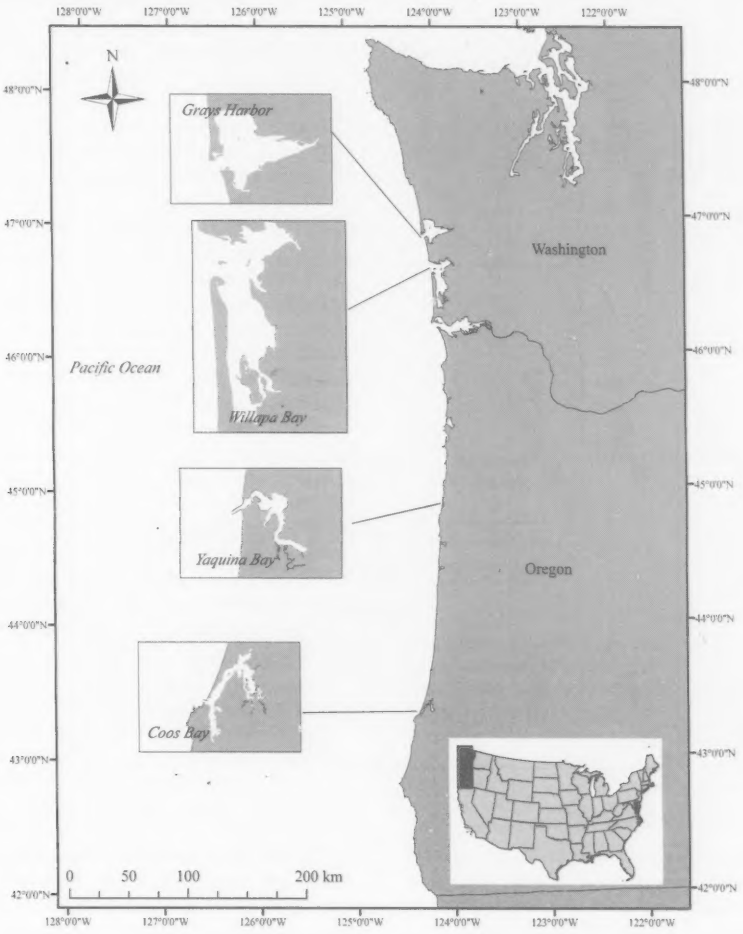

Figure 1

Map of coastal Oregon and Washington with insets showing the four estuaries studied: Grays Harbor (total subtidal area=8545 ha), Willapa Bay (total subtidal area=11,200 ha), Yaquina Bay (total subtidal area=471 ha), and Coos Bay (total subtidal area=1195 ha).

periods by approximately 50 m. Benthic organisms, including the four target flatfish species, were collected during daylight with a beam trawl (Gunderson and Ellis, 1986). The beam trawl had an effective opening width of 2.3 m and a height of 0.6 m. The net was towed at a speed of 0.8–0.9 m/s behind a 6.4-m research vessel with a minimum 5:1 scope of line out to depth. The distance towed averaged 139 m in 1998–2000. Trawls were made against the prevailing current over a variety of tide stages, although efforts were made to conduct trawling near the time of daylight slack low water. Sampling was not conducted at high current velocities during maximum ebb and flood tides to ensure the greatest adherence of the beam trawl to the substratum. All fish and invertebrates captured were identified to species and English sole were measured for total length (TL) to the closest 1.0 mm. Other species of flatfish were measured (TL) only in 1999 and 2000.

Data analysis

There was considerable variability in the data associated with each sampling period that was not related to habitat use. This variability was due to other factors, such as patterns in interannual variability in recruitment to individual estuaries or to differences in overall abundance among the four flatfish species. To minimize the effect of this variability on the analyses, it was

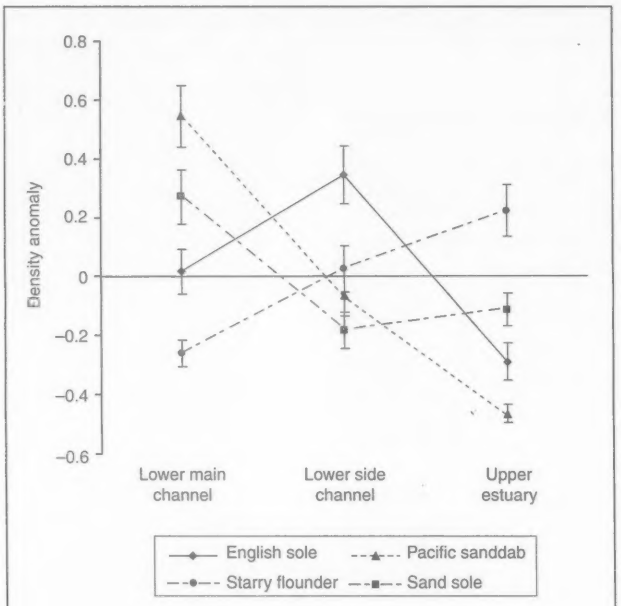

Figure 2

Average density anomaly (and standard error bars) for English sole (*Pleuronectes vetulus*), Pacific sanddab (*Citharichthys sordidus*), sand sole (*Psettichthys melanostictus*), and starry flounder (*Platichthys stellatus*) by habitat type across all study estuaries, months, and years.

necessary to standardize the data within each estuary. We used the normalized anomaly (Zar, 1974) of flatfish densities as the dependent variable to compare use of habitats within estuaries for each species, where

$$a_i = \frac{x_i - \bar{x}_{emy}}{sd_{emy}},$$

In this equation the subscript i refers to an individual density from a trawl survey site within an estuary-month-year combination, *emy* refers to the estuary-month-year combination where a trawl survey occurred, and $\bar{x}$ and sd are the mean and standard deviation of all trawl surveys occurring in that estuary-month-year combination. By using the anomaly of the densities, we reduced the variation in the data that was attributed to estuarine, seasonal, and interannual sources in order to concentrate solely on the within-estuary component of variation. For example, if the average catch of Pacific sanddab was 1000/ha for the Grays Harbor estuary in June 2000, individual trawl hauls from Grays Harbor in June 2000 with catches <1000/ha would have a negative density anomaly, whereas trawl hauls with Pacific sanddab catches >1000/ha would have a positive density anomaly.

The density anomalies were analyzed by using analysis of variance (Zar, 1974). The full model used to analyze spatial distributions of each species included the main effects of habitat type, month of survey, year of survey, and estuary, as well as estuary-habitat, month-habitat, and year-habitat interaction terms. The interaction terms were specifically included to test the hypotheses that spatial distribution of each flatfish species was consistent across estuaries, years, and months. All significant (P<0.05) main effects and interactions were compared for significant differences among effect levels by using the least squares mean approach as a *post hoc* test with a Tukey's adjustment for multiple comparisons (Zar, 1974).

Results

Juvenile Pacific sanddab collected during the trawl surveys ranged in length from 23 to 150 mm TL. The analysis of Pacific sanddab density anomalies for habitat types within estuaries resulted in significant differences among habitats in the estuaries. There were significantly higher density anomalies in lower main channel habitats and significantly lower anomalies in upper estuary sites (Fig. 2). Lower side channels usually had

negative density anomalies—the most notable exceptions being Willapa Bay and Grays Harbor in 1998 (Fig. 3). This pattern produced significant interactions between habitat and both year and estuary.

The lengths of sand sole captured by trawling were comparable to those for Pacific sanddab, ranging from 20 to 234 mm TL, and only 12 specimens longer than 150 mm TL. Sand sole catch was highly variable across all systems, and there were 318 zero catches over the total 431 trawls. Sand sole density anomalies followed a pattern similar to those of Pacific sanddab. Density anomalies were significantly higher at lower main channel sites than at other sites within the estuary (Fig. 2). Density anomalies were similar between upper estuary sites and lower side channel sites. There were no significant interaction terms between estuary or year and habitat type; thus the pattern in spatial distribution of sand sole appeared to be consistent across estuaries and years.

Starry flounder were the least common species of flatfish captured in the study estuaries. The starry flounder captured were larger than the other species of flatfish, ranging from 49 to 376 mm TL, and 44 individuals were >150 mm TL. Density anomalies were highest at upper main channel sites (Fig. 2). As with sand sole, there were no significant interaction terms between habitat type and either estuary or year. The effect of habitat type on starry flounder densities was thus a consistent effect observed across all estuaries and years.

English sole lengths ranged from 14 to 200 mm TL and only 12 individuals were greater than 150 mm TL. English sole density anomalies were significantly higher at lower side channel sites than at other estuarine locations (Fig. 2). There was also a significant interaction term between habitat type and month. In August there was no significant difference between density anomalies in lower side channel and lower main channel sites, while in June density anomalies were much larger in lower side channels than at all other locations. The significant month and habitat type interaction in the analysis of English sole density anomalies was most likely due to habitat changes observed in juvenile English sole as they grow (Rooper et al., 2003). A carrying capacity for large (>50 mm TL) English sole was observed in the study estuaries, and large English sole distribution expanded when densities were high (Rooper et al., 2003). The expansion of English sole distribution when densities were large corresponds to an increase in the density anomalies of Pacific sanddab in lower main channel areas (Fig. 4). Conversely, as large (> 50-mm-TL) English sole densities decreased, Pacific sanddab appeared to increase their distribution in the estuaries, as observed in higher density anomalies in lower side channels.

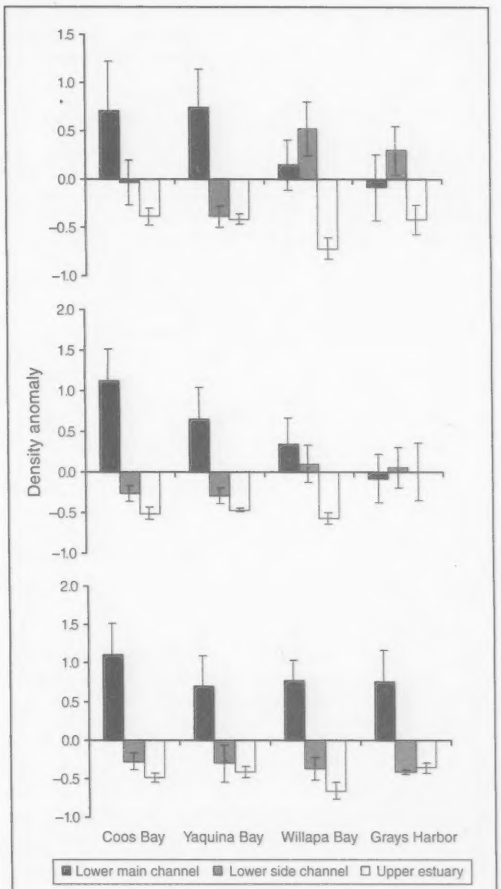

Figure 3

Pacific sanddab (*Citharichthys sordidus*) density anomalies (and standard error bars) by estuary and habitat type from 1998 (upper panel) through 2000 (lower panel).

Discussion

We observed evidence for resource portioning in four species of co-occurring juvenile flatfish in west coast nursery estuaries. The analysis of density anomalies indicated that the four flatfish species exploit different areas of estuaries. The spatial segregation among juvenile flatfish species observed in our study is consistent with results of other studies and indicates the potential for interspecific competition among the four species. Surveys of flatfish assemblages in Puget Sound, Washington have revealed spatial segregation of juvenile flatfish by depth, although the pattern was not consistent among sites (Thornburgh, 1980). In Thornburgh's study, spatial segregation may have been driven by differences in sediment type at the sites and by differences in settling times among the dominant species: English sole, sand sole, Pacific sanddab, and rock sole (*Lepidopsetta bilineata*). Distinct patterns in spatial distribution have also been observed for juvenile flatfish assemblages beyond the Pacific Northwest. In estuaries along the California

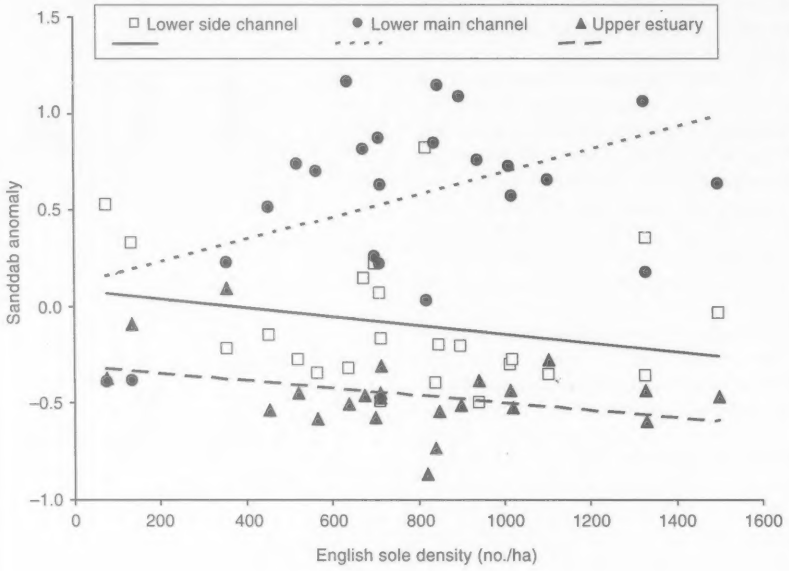

Figure 4

Average Pacific sanddab (*Citharichthys sordidus*) density anomaly compared to density of English sole (*Pleuronectes vetulus*) >50 mm TL at each location in the study from 1998 through 2000.

Bight, diamond turbot (*Hypsopsetta guttulata*) settle in the upper portions of bays during January and March, whereas California halibut (*Paralichthys californicus*) are found closer to bay entrances and the open coast, settling from March to September (Kramer, 1991). Settlement timing has also been found to be an important partitioning factor for common dab (*Limanda limanda*) and plaice (*Pleuronectes platessa*) in a small Scottish bay, where plaice settle earlier in the year than dab (Steele and Edwards, 1970). Depth has been identified as an important factor in partitioning nursery areas for the common dab and age-0 plaice (Edwards and Steele, 1968; Gibson, 1973). Juvenile flatfish in Alaskan inlets have also been found to segregate with depth and a number of other factors, such as temperature and sediment type (Norcross et al., 1997). Habitat type has also been found important in determining the spatial segregation of northeast Atlantic flatfish assemblages; ontogenetic shifts in habitat use occur in some species (Walsh et al., 1999; Phelan et al., 2001).

These studies indicate that flatfish species that exist together in nursery areas can partition resources in a number of ways according to biological (i.e., diet) or physical (i.e., depth or salinity) requirements, or according to a combination of both biological and physical requirements. Studies of shallow water habitats have generally indicated that flatfish in nursery areas are not limited by food resources (Evans, 1983). In west coast estuaries food resources can be quite high, especially in intertidal areas (Gunderson et al., 1990; Dumbauld et al., 2000). After review of diet studies documenting feeding differences among Pacific sanddab and English sole (Hogue and Carey, 1982; Thornburgh, 1980), as well as the abundance of food within the nursery area, we do believe it is unlikely that direct competition for food is solely responsible for the apparent pattern in estuarine distributions between the two species. We suggest that the segregation observed in northwest estuaries is most likely caused by differences in physical conditions of the habitat.

The four species of flatfish observed in the present study probably partition the nursery estuaries along gradients of salinity and temperature. Starry flounder were found in upper reaches of the estuary to a greater degree than the other species—a finding that is consistent with their ability to tolerate low salinity (Orcutt, 1950). Starry flounder were most abundant in Yaquina Bay, where the coverage of trawl survey sites extended farther up the estuarine salinity gradient than in other estuaries. The average salinity in June was 16–18 ppt at the uppermost Yaquina Bay sites, whereas the average June salinity at sites in other estuaries was always greater than 19 ppt. Salinity has been found to be an important determinant of the distribution of other flatfish species (Coggan and Dando, 1988; Marchand, 1988; Kerstan, 1991; Gibson, 1994; Marshall and Elliot, 1998).

The temperature preferences of English sole may allow them to exploit areas of the estuary not used extensively by Pacific sanddab. Temperatures less than 17.5°C have been observed to lead to high English sole growth (Yoklavich, 1982). These temperatures were observed in lower side channels of the study estuaries. For the speckled sanddab (*Citharichthys stigmaeus*), a close relative of the Pacific sanddab, maximum growth has been observed from 8° to 13°C (Ehrlich et al., 1979). This temperature range is closer to the temperatures found in lower side channels, and lower than the temperature range found in lower main channels in our study area. Thus, the Pacific sanddab, if it has temperature tolerances similar to those of its congener, may be limited to lower main channel locations in order to optimize growth rates, whereas optimal English sole growth occurs at the higher temperatures found in lower side channels.

An alternative explanation for Pacific sanddab distribution may be found in its response to high English sole density. The changing distribution of Pacific sanddab, when confronted by high densities of English sole, provides evidence that competition may occur between these two species. When English sole densities are high, Pacific sanddab seem to be limited in distribution to lower main channel locations (sites not preferred by English sole), and when English sole densities are low, Pacific sanddab appear to be more evenly distributed throughout the estuary. This pattern does not apply to starry flounder or sand sole, whose distributions remain the same regardless of English sole density. The implication of this resource partitioning is that English sole year-class strength may be affecting the ability of Pacific sanddab to use areas of the estuaries where conditions are optimal for flatfish growth.

Distinct patterns of habitat use by juvenile English sole, starry flounder, sand sole, and Pacific sanddab were observed in all four estuaries that we examined. Highest densities of Pacific sanddab and sand sole were found in lower main channel sites, highest densities of English sole were found in lower side channels, and highest densities of starry flounder were found in upper estuarine sites. These patterns of spatial segregation were consistent from 1998 through 2000. The patterns were consistent across the four estuaries encompassing 400 km of coastline. Resource partitioning is probably based primarily on temperature and salinity tolerances and growth preferences of the individual flatfish species; however, there is evidence of competition between English sole and Pacific sanddab when their spatial distributions are examined in response to their relative abundances.

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Length-specific brood size and winter parturition in pink seaperch (*Zalembius rosaceus*) (Perciformes: Embiotocidae)

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The viviparous pink seaperch (*Zalembius rosaceus*) is considered unusual among other embiotocids because of its deep-water habitat (Tarp, 1952), winter parturition (Goldberg and Ticknor, 1977), small brood size (Baltz, 1984), and apparent lack of a positive relationship between brood size and female size (Baltz, 1984). In the present study, I present further support that parturition in pink seaperch occurs in winter and new evidence indicating length-specific brood sizes in the species.

Pink seaperch are found in deep water (to 229 m: Miller and Lea, 1972) over soft bottom (Allen, 1982) year-round off the coasts of California and Baja California (Eschmeyer et al., 1983). Mating occurs in spring and parturition occurs in winter (Goldberg and Ticknor, 1977)—a unique breeding schedule among surfperches. Other surfperches mate in summer or fall and give birth the following spring or summer when food for offspring is plentiful. For reasons that remain unclear, brood size for pink seaperch is considered low (mean=3.5: Goldberg and Ticknor, 1977) compared to other small-size (<160 mm) surfperches (reviewed in Baltz, 1984).

A positive relationship between brood size and female size is generally the rule among fishes (Bagenal, 1978) and is observed in all surfperches with the exception of pink seaperch (Baltz, 1984). However, data for the species are dubious because near-term females tend to abort their young during the time of collection (Baltz and Knight, 1983; Baltz, 1984)—a behavior that can result in both underestimates in brood sizes and high variability in length-specific brood size.

The goal of this study was to evaluate characteristics of the reproductive biology of pink seaperch using samples taken during periods both early and late in the breeding season. I predicted that estimates in length-specific brood size for females collected later in the season should be significantly smaller than those collected earlier if, in fact, near-term females have a high probability of aborting embryos. Similarly, I expected to see higher variability in relationships between length-specific brood size and female size in the late, compared to early, period of the breeding season.

Materials and methods

Specimens of female pink seaperch were collected with a 7.6-m (headrope) otter trawl with 1.3-cm codend mesh on the Palos Verdes shelf near Point Fermin, CA (33°41′N, 118°19′W) in fall (September and October, at 54 and 60 m depth, respectively) 1994 and in winter (January, at 66 m depth) 1995. Females were distinguished from males by having either a rounded belly or by lacking a fleshy reproductive organ on the anterior portion of the anal fin (Tarp, 1952). Gravid females collected in winter were stored separately in sealable bags to ensure that any embryos subsequently born were included in brood size records; females collected in fall had no evidence of premature births nor were there any premature embryos present in fall collections (see Results section). Individuals were placed on ice, frozen, and processed within 10 days. Females were dissected and the following information was recorded: standard length (SL ±1 mm), body mass (±1 g), brood size, embryo SL (±1 mm), embryo mass (±0.01 g), and evidence of premature birthing. From the appearance of females that had evidently expelled their broods while in storage bags, I recorded a female as having prematurely given birth if her ovary was devoid of embryos, flaccid, and contained traces of fresh blood. The relationships between female and brood size for fall and winter were analyzed separately by using regression analyses (SPSS, vers. 10, SPSS, Inc., Chicago, IL). Females showing evidence of recent expulsion were not included in brood size analyses.

Results

The size distribution of females captured varied between seasons (Fig. 1). The mean standard length (SL) of females in fall and winter was 125 mm (±15 mm SD, n=27) and 96 mm (±21 mm SD, n=76), respectively, and this difference was significant (t-test: t=6.82, df=101, P<0.001). All females greater than or equal to 100 mm SL (n_{fall}=26, n_{winter}=31) were sexually mature, having either embryos or evidence of recent expulsion of embryos. Among the mature females, the mean SL in fall and winter was 127 mm (±14 mm SD, n=26) and 117 mm (±9 mm SD, n=31), respectively, and this difference was also significant (t-test: t=3.19, df=55, P=0.002).

Both mean brood size and the relationship between female size and brood size varied between seasons (Fig. 2A). Mean brood sizes in fall and winter were seven (±3 SD) and three (±1 SD), respectively, and this

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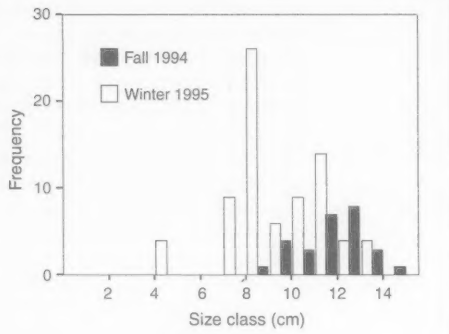

Figure 1

Size distribution for mature female pink seaperch (*Zalembius rosaceus*) (n=103) collected in fall 1994 (black bars) and winter 1995 (white bars). Bars represent 1-cm size classes.

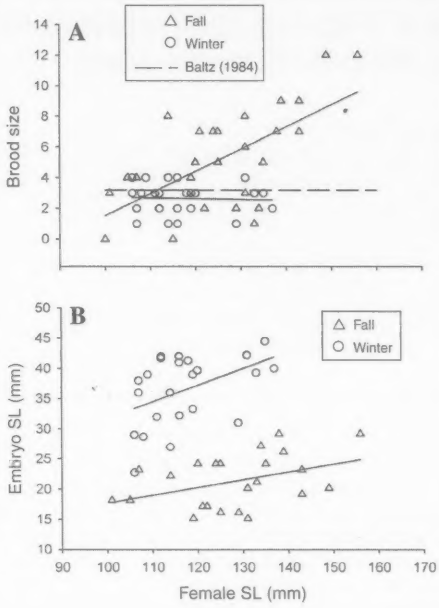

Figure 2

Linear regressions of (**A**) brood size (fall: r^2=0.39, brood size=−12.9 + 0.14x, n=26; winter: r^2= 0.00, n=31), and (**B**) embryo size (fall: r^2=0.17, embryo SL=4.9 + 0.13x; winter: r^2=0.20, embryo SL=4.2 + 0.28x) on female size for fall (triangles) and winter (circles) collections of pink seaperch (*Zalembius rosaceus*). Dashed line in A represents data from Baltz (1984).

difference was significant (t-test: t=5.15, df=55, P<0.001). The incidence of premature births for winter females was 18% (seven of 38 females) compared to 0% (0 of 27 females) for fall females, and differed significantly (Fisher's exact test: P=0.04). Female size was a good predictor of brood size in fall but not in winter (fall: r^2=0.39; winter: r^2=0.00, Fig. 2A).

Embryos were more developed and larger in winter than fall, and larger females brooded larger-sized embryos (Fig. 2B). Fall embryos had a mean SL of 21.3 mm (±4.2 mm SD) and were characterized by pale pink coloration, translucent tissue, and the absence of distinct scales. Winter embryos had a mean SL of 36.4 mm (±5.8 mm SD) and had firm and opaque tissue, distinct scales, iridescent pink coloration, and appeared as miniature adults. In both fall and winter, linear regressions of embryo-on-female size were significant (fall: r^2=0.17; winter: r^2=0.20, Fig. 2B).

Discussion

Both embryo characteristics and female reproductive condition provided evidence of winter parturition in pink seaperch and confirmed conclusions made by Goldberg and Ticknor (1977). Winter embryos had advanced morphological characteristics similar to those of adults, compared to embryos examined in fall, and were similar in size to those reported by Goldberg and Ticknor (1977). Evidence of a relatively high incidence of abortion and presence of many embryos (n=51) in winter collections provided further evidence that parturition occurs in or around January. Winter parturition is unique among surfperches yet no studies, to the author's knowledge, have provided an explanation for the unusual breeding schedule of pink seaperch.

Results from this study demonstrate a positive relationship between brood size and female size in pink seaperch, contrary to results of previous reports. Brood size increased with female size in fall but not in winter (Fig. 2A) in this study. The lack of a relationship observed in winter was similar to previous conclusions (See Fig. 2 in Baltz, 1984). Baltz and others (Goldberg and Ticknor, 1977; Baltz and Knight, 1983) speculated that sample effects may have explained the lack of a relationship between brood size and female body size, but no clear evidence was provided. In the present study, there was a high incidence of females (18%) that had aborted all embryos (i.e., complete abortion) among winter collections, and these females were excluded from analyses. However, partial abortions may occur in embiotocids (Schultz, 1993) presenting the possibility of underestimating brood size. Females with partially aborted broods were not identified nor excluded from the present study. Therefore, if such behavior occurred among large winter females, it would provide a reasonable explanation for the lack of relationship observed between brood size and female size.

Winter females had larger brood sizes than their fall counterparts and a higher frequency of abortion, providing evidence that winter females had partial rather than complete broods. Individuals smaller than the

mesh size of the net were present in winter collections, probably aborted by females stressed during capture. The number of embryos (n=51) present in the winter collections was higher than would be expected if they had been aborted by females having shown evidence of complete abortions (n=7). Therefore, pink seaperch have length-specific brood sizes as observed in other surfperches, and this finding is supported by the more reliable fall data from the present study.

Mean brood size for pink seaperch in the present study was higher than previously reported for the species. Goldberg and Ticknor (1977) reported that females had an average brood size of 3.5, which was similar to mean brood sizes obtained for winter collections in this study; however, according to arguments already presented, winter data likely resulted in an underestimation of brood size. Both mean and maximum fall brood sizes (max=10) were greater than winter brood sizes and greater than the brood size in samples examined in Goldberg and Ticknor's (1977) study. If brood size estimates in the Goldberg and Ticknor (1977) study included females collected in winter, the authors probably underestimated brood size, as well. The mean brood size of pink seaperch is similar to that of other deep water fishes (Koslow et al., 2000) but is considered relatively small compared to other embiotocids (reviewed in Baltz, 1984).

An unexpected result from the present study was evidence that large female pink seaperch have an earlier breeding schedule than small females. Reproductively active females in fall were larger on average than winter females (Fig. 1), indicating that large females left breeding sites earlier or that small females arrived at breeding sites later. Although greater temporal resolution of changes in size distribution would have been desirable, further evidence for size-dependent breeding was apparent from female- and embryo-size relations. In both fall and winter, embryos in large females were larger than embryos in small females (Fig. 2B), which would be expected if the reproductively active females in fall bred earlier than those in winter. An alternative explanation for the positive relationship between female size and embryo size would be that embryos in large females develop faster than those in small females because of greater maternal investment. I did not have sufficient data on embryo development because this was not the focus of my study; however, it is a hypothesis that warrants further investigation. Delayed breeding by smaller females of pink seaperch is a pattern observed in other surfperches (Eigenmann and Ulrey, 1894; Hubbs, 1921; Schultz, et al., 1991) and may arise from both energetic limitations on the time of reproduction and fitness advantages accrued by postponing reproduction and diverting additional energy towards growth (Schultz, et al., 1991).

Acknowledgments

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Aging fish otoliths recovered from Pacific harbor seal (*Phoca vitulina*) fecal samples

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Seals and sea lions are opportunistic predators that feed on a variety of fish and cephalopods, including some commercially and recreationally important species. Concerns over their interactions with commercial and sport fishing operations, and other human activities, has a long history in the Pacific Northwest (Everitt and Beach, 1982). The perceived increase in such interactions led, in part, to the U.S. Congress amending the Marine Mammal Protection Act (MMPA) in 1994. Chief among the amendments was a call for research to determine 1) whether California sea lions (*Zalophus californianus*) and Pacific harbor seals (*Phoca vitulina*) were affecting the recovery of listed or depleted salmonids, and 2) what broader impacts they may have on the coastal ecosystems of Oregon, Washington, and California (NMFS, 1997). In this note, we begin to address the latter question. Specifically, we describe a novel application of otolith aging techniques that can be used to increase the understanding of pinniped foraging ecology and, thus, their potential impact on the fishery resources of coastal ecosystems.

The Oregon Department of Fish and Wildlife's (ODFW) Marine Mammal Research Program has studied harbor seal foraging habits since the mid-1980s, primarily through the collection and analysis of scat (fecal) samples (Riemer and Brown, 1997; Riemer et al.[1]; Wright et al.[2]). Our results, as well as those from other pinniped food habit studies in Oregon (Graybill, 1981; Brown and Mate, 1983; Roffe and Mate, 1984; Orr et al., 2004), indicate that these animals consume a large number of diverse prey species. Concurrent research in Oregon indicates that Pacific harbor seals have increased significantly following protection under the MMPA; Brown et al. (2005) estimated that the 2002 statewide population total was 10,087 individuals. As noted above, these types of increases in pinniped abundance have led to more frequent interactions with coastal fish resources and hence an increased interest in the composition and abundance of prey in their diet.

Fortunately, new techniques have recently been developed to analyze pinniped diets. For example, rather than using traditional methods that rely strictly on otoliths (fish ear bones) for identifying prey, many researchers now try to identify all skeletal structures recovered from scats, which provide a more complete picture of pinniped diets (Olesiuk et al., 1990; Cottrell et al., 1996; Riemer and Brown, 1997; Browne et al., 2002). In addition, researchers are beginning to use molecular genetic methods to provide greater resolution in determining diet composition (Purcell et al., 2004; Deagle et al., 2005; Kvitrude et al., 2005). In this note, we add to this growing list of techniques by describing a novel use of fish otolith aging techniques to further our understanding of pinniped diets.

Fisheries scientists have aged fish otoliths to aid in the management of commercial and recreational fisheries (Love et al., 2002). Marine mammal scientists, on the other hand, have relied upon the identification of otoliths recovered from scats to identify the prey of pinnipeds (Brown and Mate, 1983; Beach et al.[3]; Harvey, 1989; Pierce and Boyle, 1991). However, the age of prey has rarely been considered when describing seal and sea lion diets. We believe that estimates

[1] Riemer, S. D., R. F. Brown, B. E. Wright, and M. Dhruv. 2001. Monitoring pinniped predation on salmonids at Alsea River and Rogue River, Oregon: 1997–1999. Unpubl. Contract Rep. to Pacific States Marine Fisheries Commission, NOAA Grant No. NA87FX0464, 38 p. [Available from OR Dept. Fish. and Wildl., 7118 NE Vandenberg Ave., Corvallis, OR 97330.]

[2] Wright, B. E., R. F. Brown, S. D. Riemer, and A. M. Ougzin. 2002. Pinniped predation on adult salmonids in the Alsea Estuary, Oregon. Unpubl.Contract Rep. to Pacific States Marine Fisheries Commission, NOAA Grant No. NA17FX1603, 35 p. [Available from OR Dept. Fish. and Wildl., 7118 NE Vandenberg Ave., Corvallis, OR 97330.]

[3] Beach, R. J., A. C. Geiger, S. J. Jeffries, S. D. Treacy, and B. L. Troutman. 1985. Marine mammals and their interactions with fisheries of the Columbia River and adjacent waters, 1980–1982. NWAFC (Northwest Alaska Fisheries Science Center) processed rep. 85-03, 316 p. NWAFC, National Marine Fisheries Service, Northwest Region, 7600 Sand Point Way N.E., Seattle, WA 98115-0070.

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of the age of prey will result in a more comprehensive picture of pinniped diets and help to augment stock assessments that use age-specific models. We report our application of these techniques to Dover sole (*Microstomus pacificus*) otoliths recovered from Pacific harbor seal scat samples collected in an Oregon estuary. Dover sole were selected as a case study because they are a common prey of harbor seals in Oregon (Riemer and Brown, 1997) and their otoliths have been aged successfully in previous studies (Hagerman, 1952; Brodziak and Mikus, 2000).

Materials and methods

We conducted our study during the spring and summer of 1996, and year-round from 1997 through 2002, in the Alsea Estuary located near Waldport, Oregon (44°26′N, 124°3′W). The local harbor seal population in this area consisted of approximately 600 animals throughout the study period. Scat samples from this population were obtained during low tides by approaching haul-out areas on foot or by boat, and slowly moving the animals into the water. Samples were placed in individually labeled plastic bags and frozen. The number of scat samples collected during each trip varied depending on the number and location of animals hauled out, and on weather and ocean conditions.

Scats were thawed and partially dissolved in water, then rinsed through a series of nested sieves (2 mm, 1 mm, 0.71 mm). All prey hard parts (e.g., otoliths, bones) recovered were dried and placed in individually labeled jars. Prey species were identified from all prey hard parts recovered from each sample. Dried hard parts were examined under a dissecting microscope and identified by using a comparative collection of fishes from the northeast Pacific Ocean and Oregon estuaries. Otoliths and diagnostic bones were identified, counted, and the side (left or right) was noted to estimate a minimum number of individuals (MNI) represented in each sample by following the procedures described by Lance et al.[4]

Otoliths selected for aging were given individual identification numbers and stored in gelatin capsules. One sample with 65 similarly size otoliths was subsampled by randomly selecting the first 18 otoliths recovered. Before aging, otoliths were measured to the nearest mm for total length, width, and length of sulcus by using an optical micrometer. Degree of erosion (level 1 having the least amount of erosion and level 3 having the greatest) was recorded by following techniques described in Tollit et al. (1997). Reference photographs were taken of each otolith with a dissecting microscope and digital camera before age estimates were determined.

Final otolith ages were determined by using one of two techniques. First, all fish otoliths were submerged in a dish of ethanol with a black background and annuli were counted under a dissecting microscope with reflected light (i.e., surface aged). Second, fish ≥ four years were re-aged according to the method described in Pikitch and Demory (1988) (i.e., break-and-burn method). The first annulus deposited was determined to be the completion of growth for the first year following the convention for aging adult Dover sole (Chilton and Beamish, 1982). In some cases, a mark within the otolith core was counted as the initial increment because it met the identification criteria for an annual increment.

Results

Dover sole remains (bones and otoliths) were recovered from 296 of the 3370 harbor seal scat samples collected during the study period (Table 1). Dover sole otoliths were recovered from 132 of these scat samples. Eighty-nine of these otoliths (21%) were excluded from our analyses because of poor condition (erosion or breakage), extremely small size, or because they had been randomly subsampled. The majority of otoliths were moderately eroded (level 1: 16%, level 2: 64% and level 3: 20%).

Of the 339 otoliths analyzed, 98.2% were assigned an age; 71.2% (237) by surface aging and 28.8% (96) by the break-and-burn method. Six otoliths were excluded from age estimates because of extreme edge wear and erosion. Forty-nine (92.5%) of the scats with more than one otolith analyzed resulted in fish of multiple ages.

The majority (70.6%) of otoliths analyzed were from one-, two-, and three-year-old fish; the rest were from four to six year-old (25.8%) and seven to 12 year-old (3.6%) (Table 1). Of the juvenile fish otoliths recovered, the presence of one- and two-year-old fish peaked in July, and three-year-old fish were found most frequently in August. Three of the four oldest fish otoliths were recovered during the summer months, and one 10-year-old fish was recovered in May. The scat samples collected during fall (September–November) primarily included two- and three-year-old fish (72.5%).

Aging otoliths of Dover sole increased MNI in harbor seal scats by 13% (269 versus 238). In most cases the number of Dover sole increased by one fish per scat when using both age and otolith side to enumerate MNI.

Discussion

We have shown in the present study that 1) Dover sole otoliths recovered from harbor seal scats can be successfully aged, and 2) seals in the Alsea River consumed Dover sole that ranged in age from one to 12 years. Interestingly, the highest frequency of occur-

[4] Lance, M. M., A. J. Orr, S. D. Riemer, M. J. Weise, and J. L. Laake. 2001. Pinniped food habits and prey identification techniques protocol. AFSC (Alaska Fisheries Science Center) Proc. Rep. 2001-04, 36 p. Alaska Fisheries Science Center, NMFS, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

Table 1

Age distribution for Dover sole (*Microstomus pacificus*) consumed by harbor seals (*Phoca vitulina*), based on otoliths recovered from scats collected in the Alsea Estuary, Oregon. Total number of scats collected (*n*), scats with Dover sole bones and otoliths (*n*-Dover), and otoliths only (*n*-otoliths), and the number of Dover sole otoliths recovered (*n*) and successfully aged (*n*-aged) were pooled monthly over all years from 1996 through 2002.

	Scat			Otolith		Age (yr)												
Month	*n*	*n*-Dover	*n*-otoliths	*n*	*n*-aged	1	2	3	4	5	6	7	8	9	10	11	12	%[1]
Jan	33	0																0%
Feb	24	1	1	3	3		1	2										0.9%
Mar	103	2																0%
Apr	212	12	1	0	0													0%
May	230	22	11	12	11		6	2		2					1			3.3%
Jun	423	26	16	38	35	4	9	9	4	5	1	2		1				10.5%
Jul	347	91	40	174	118	26	32	23	18	11	6		1		1			35.4%
Aug	330	65	32	102	97	11	23	35	15	7	2		3				1	29.1%
Sep	806	54	21	65	55	1	23	17	7	4	2		1					16.5%
Oct	387	21	8	13	10	1	5	3				1						3.0%
Nov	173	2	2	20	4			2	1	1								1.2%
Dec	0																	0%
Total	3370	296	132	428	333	43	99	93	45	30	11	3	5	1	2	0	1	333

[1] Percentage of otoliths aged by month.

rence for Dover sole in our collections (ODFW[5]), and the greatest range in their age (Table 1), occurred during summer—a period when Dover sole move into shallow nearshore waters (Hagerman, 1952; Markle et al., 1992). This migration into nearshore waters brings fish into contact with an increasing population of pinniped predators.

The majority of Dover sole otoliths recovered from scats were those of fish younger than four years. In contrast, Dover sole landed in Oregon's commercial fishery between 1984 and 2004 were aged to be between three and 60 years old and the average age was 13 years (ODFW[5]). Of the 45,026 fish aged from the commercial fishery, over 50% were ages similar to those recovered from seal scat samples (four to 12 years) and had an average length of 33.4 cm. Of the fish checked, 79% were identified as mature. However, the majority (70.5%) of otoliths analyzed in our study were from one, two-, and three-year-old fish, whereas only one of the commercially caught fish was in this age range. Four- to six-year-old fish made up 0.3% of the commercially sampled fish and seven- to 12-year-olds made up the largest portion at 53.5%. This lack of younger age fish in the commercial fishery is partly due to the discarding of smaller unmarketable fish at sea. Sampson and Wood (2001) reported that from 1956 through 2000, between 5% and 14.6% of the commercial Dover sole catch at sea was discarded because of the small unmarketable size of the catch. What effect a consistent removal of older age fish and the discarding of younger fish by the commercial fishery, coupled with the take of younger age fish by an increasing number of predators could have on the population as a whole, is unknown.

Many species of marine fishes other than Dover sole contribute to important commercial fisheries in Oregon (ODFW[6]). Estimating prey age from fish otoliths recovered from seal and sea lion scats will be useful for researchers when describing impacts on long-lived marine species such as rockfish, which may be at greater risk to this long-term and increasing predation by coastal pinnipeds. Love et al. (2002) reported that rougheye rockfish (*Sebastes aleutianus*) live to at least 205 years and yelloweye rockfish (*S. ruberrimus*) to 118 years, whereas other species such as calico (*S. dalli*) and squarespot (*S. hopkinsi*) may only live for a decade or two. These older fish in some cases also have a late maturity; for example, only half of all yelloweye rockfish are mature at an age of 22 years.

As the sustainability of these species and the fisheries that target them become difficult to manage, there will be more interest in the impact of predators on these fish populations. Determining fish age has enabled biologists

[5] ODFW (Oregon Department of Fish and Wildlife). 1984–2004. Unpubl. data. [Data are on file at Oregon Department of Fish and Wildlife Newport-Marine Program office, 2040 S.E. Marine Science Drive, Newport, Oregon 97365.]

[6] ODFW (Oregon Department of Fish and Wildlife). 2000. Oregon Marine Fisheries 2000 status report, 109 p. [Available from Oregon Department of Fish and Wildlife Newport-Marine Program office, 2040 S.E. Marine Science Drive, Newport, Oregon 97365.]

to more accurately estimate appropriate fishing levels, particularly for rockfish species (Love et al., 2002). This information can also contribute to assessing the impact of pinnipeds on these species and can improve stock assessment models. Otolith age can provide information on the size of fish consumed when the age-length composition in the population or subgroup is available (Salthaug, 2003). In addition, age estimates provide information on the reproductive maturity of the prey consumed. Aging will also provide a more accurate estimate of the MNI of a particular prey species consumed than an estimate based on the maximum number of left or right otoliths of a similar size, particularly because different age fish can have otoliths of approximately the same size.

Researchers should note that the digestive process does cause erosion of otoliths and can result in underestimation of fish ages. We did not attempt to determine how otolith-based age estimates were affected by erosion, but a carefully designed captive feeding study would be able to address this issue in the future. However, because there are few other methods to determine the age distribution of fish taken by pinnipeds, this technique is useful when describing the diet of seals and sea lions.

Acknowledgments

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Habitat, age, and diet of a forage fish in southeastern Alaska: Pacific sandfish (*Trichodon trichodon*)

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Forage fish are an important part of Alaska's marine ecosystems and coastal areas. Forage fish are a critical food source for numerous groundfish, marine mammals, and seabirds (Wespestad[1]; Allen and Smith, 1988; Paul et al., 1997; Yang and Nelson, 2000; Mecklenburg et al., 2002). Little is known, however, about the life history characteristics or habitat of many forage fish species in Alaska, including Pacific sandfish (*Trichodon trichodon*; Fig. 1). Only two articles have been published on the life history characteristics of Pacific sandfish in Alaska. Paul et al. (1997) investigated size-weight-age profiles, size at maturity, and fecundity of Pacific sandfish in the northern Gulf of Alaska, and Bailey et al. (1983) examined size and diet of juvenile (<55 mm fork length [FL]) Pacific sandfish in southeastern Alaska. Some Pacific sandfish catch data are also available for the Bering Sea, Prince William Sound, and southeastern Alaska (Isakson et al., 1971; Orsi and Landingham, 1985; Allen and Smith, 1988; Brodeur and Livingston, 1988; Sturdevant et al.[2], Orsi et al., 2000). Pacific sandfish burrow into sand, usually at depths shallower than 150 m, and can reach a maximum size of about 300 mm (Marliave, 1980; Mecklenburg et al., 2002).

Pacific sandfish are commonly found in nearshore waters of the southeastern Bering Sea and Gulf of Alaska. There is no commercial fishery for Pacific sandfish in Alaska, but sailfin sandfish (*Arctoscopus japonicus*) are commercially fished and cultured in Japan and Korea (Okiyama, 1990). In particular, information is scarce on the biology and habitat of Pacific sandfish, especially for southeastern Alaska. Shoreline development and global climate change (e.g., increased water temperature and sea level) may adversely affect Pacific sandfish populations because of the relatively specialized nearshore spawning sites and one-year incubation period of this species (Marliave, 1980).

The focus of our study was to provide new information on the general biology of a little known forage fish species. Objectives were to determine habitat preference, age, size, and diet of Pacific sandfish. To accomplish this, from 2001 to 2004, we captured Pacific sandfish with a beach seine in July and March and with a mid-water trawl in May near The Brothers Islands in southeastern Alaska.

Materials and methods

Fish capture and habitat

Pacific sandfish were captured with a beach seine at The Brothers Islands in southeastern Alaska (Fig. 2). We seined 10 sites in summer (July 2001–2003) and in winter (March 2002–2004) in a variety of nearshore habitat types (Table 1). Habitats sampled included steep bedrock outcroppings, rocky bottoms with understory kelps (e.g., *Laminaria*), eelgrass (*Zostera marina*), and sand beaches. We used a 37-m variable-mesh beach seine that tapered from 5 m wide at the center to 1 m wide at the ends. Outer panels were each 10 m of 32-mm stretch mesh, intermediate panels were each 4 m of 6-mm square mesh, and the bunt was 9 m of 3.2-mm square mesh. We set the seine as a "round haul" by holding one end on the beach, backing around in a skiff with the other end to the beach about 18 m from the starting point, and pulling the seine onto shore. The seine had a lead line and a float line so that the bottom contacted the substratum and the top floated on the surface. All seine sites were sampled during daylight and within two hours of low tide (range +1.0 to −1.5 m below mean lower low water). After retrieval of the net, the entire catch was sorted, identified to species, counted, and a subsample was measured for length.

[1] Wespestad, V. G. 1987. Population dynamics of Pacific herring (*Clupea pallasii*), capelin (*Mallotus villosus*), and other coastal pelagic fishes in the eastern Bering Sea. *In* Forage fishes of the southeastern Bering Sea; proceedings of a conference, November 1986, Anchorage, AK, p. 55–60. U.S. Dep. Interior, Minerals Management Service, OCS Study MMS 87-0017.

[2] Sturdevant, M. V., T. M. Willette, S. C. Jewett, E. Debevec, L. B. Hulbert, and A. L. J. Brase. 1999. Forage fish diet overlap, 1994–1996. APEX Project: Alaska predator ecosystem experiment in Prince William Sound and the Gulf of Alaska, 103 p. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 98163C), Auke Bay Laboratory, National Marine Fisheries Service, 11305 Glacier Highway, Juneau, Alaska.

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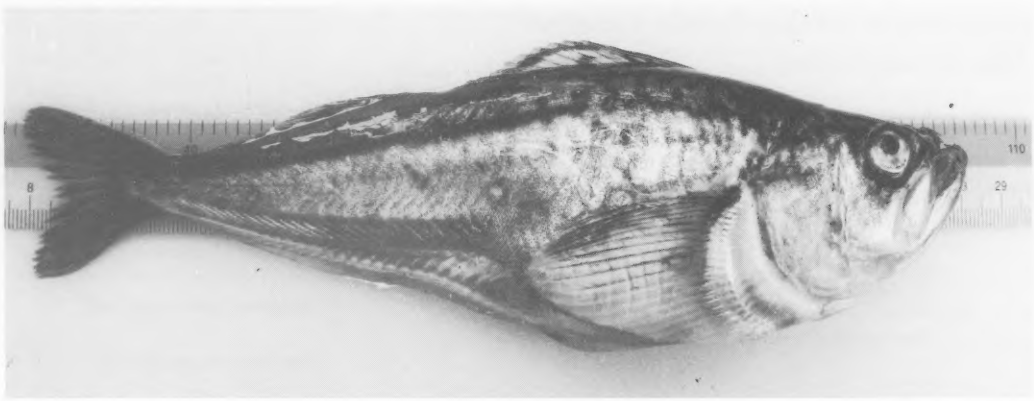

Figure 1
Pacific sandfish (*Trichodon trichodon*) captured in southeastern Alaska.

Table 1
Habitat characteristics of sites (see Fig. 2) at The Brothers Islands in southeastern Alaska where Pacific sandfish (*Trichodon trichodon*) were captured with a beach seine from 2001 to 2004. Substrata are listed in decreasing order of abundance from left to right. For vegetation, algae were mostly *Ulva*, eelgrass was *Zostera marina*, and kelps were mostly Laminariales (e.g., *Laminaria*, *Alaria*, and *Cymathere*). PSS = practical salinity scale. Catch = number of sandfish.

						Catch	
Site	Substrate	Vegetation	Slope	Temperature (°C)	Salinity (PSS)	July 2001–03	March 2002–04
1	sand, shell	algae	gentle	4.0–9.5	32–33	6	110
2	large cobble, small cobble, gravel, shell	kelp	moderate	9.0	33	14	0
3	large cobble, sand	kelp	gentle	12.0	24	1	0
4	sand, shell, gravel, small cobble	eelgrass	gentle	12.0	33	1	0
5	small cobble, large cobble, sand, gravel	kelp	moderate	4.9–9.5	33	2	1
6	bedrock outcrop	kelp	steep	4.2–10.0	31–33	900	300
7	bedrock outcrop	kelp	steep	4.2–10.0	31–33	68	500
8	bedrock outcrop	kelp	steep	4.2	33	0	1120
9	bedrock outcrop	kelp	steep	4.0	33	0	5000
10	bedrock outcrop	kelp	steep	4.0–10.0	30–33	35	7200
					Total	1027	14,231

The number of larvae (≤30 mm) in large catches in winter was estimated visually. Water temperature and salinity (practical salinity scale; PSS) were measured at each site at a depth of 20 cm with a thermometer and a hand-held refractometer.

Pacific sandfish were also captured with a mid-water rope trawl in May 2001 in Frederick Sound, midway between the mouth of Pybus Bay and The Brothers Islands, and in May 2003 in Pybus Bay (about 12 km from The Brothers Islands) (Fig. 2). In 2001, the midwater trawl was a 164 Nordic rope trawl with 1.5-m^2 alloy doors; it was 7 m high and 17 m wide and was equipped with a 19-mm codend liner. In 2003, because a different vessel was used, the trawl was a mesh wing 25/21/64

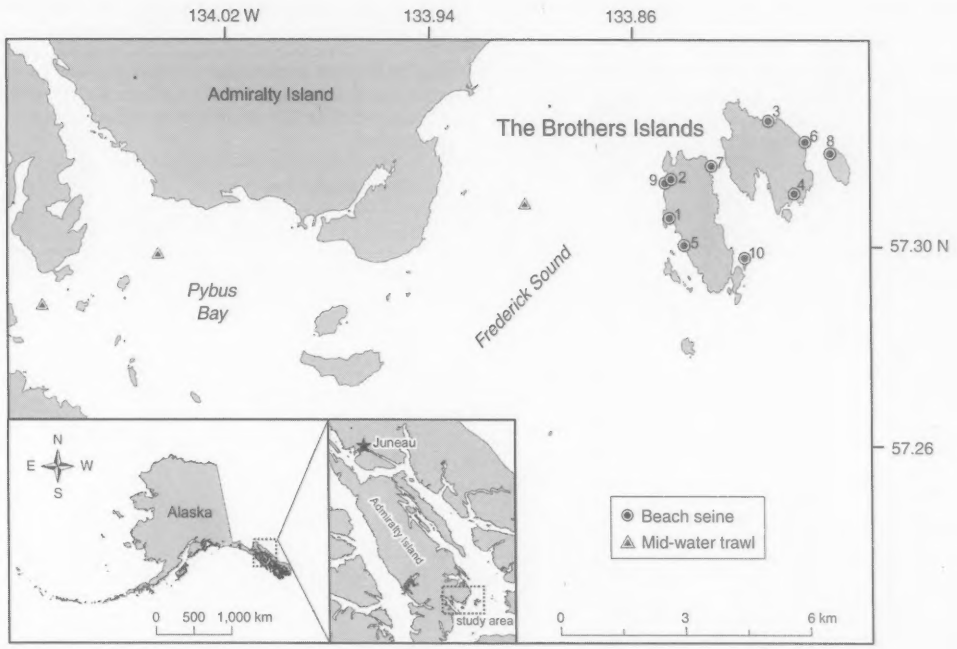

Figure 2

Location of sites (see Table 1 for habitat characteristics) sampled for Pacific sandfish (*Trichodon trichodon*) near The Brothers Islands, southeastern Alaska, 2001 to 2004. Sampling methods included beach seining and mid-water trawling.

trawl with 3.0-m^2 alloy doors; it was 11 m high and 29 m wide and was equipped with a 32-mm mesh codend liner. In Frederick Sound, water depth was about 74 m, and the trawl was fished at a depth of 14 m. In Pybus Bay, water depth was about 70 m and the trawl was fished at depths from 50 to 64 m about 400 m offshore. Water temperature and salinity were obtained from deployment of a CTD (conductivity-temperature-depth) profiler in Pybus Bay in 2003.

Age and size

A sample of Pacific sandfish was frozen and brought to the laboratory where sagittal otoliths were removed and stored in 95% ethanol. Fish used for otolith collections covered a range of sizes in the catch (Table 2). Fish were measured to the nearest mm FL, and larvae were measured to the nearest mm total length (TL). A sample of fish was individually weighed to the nearest gram. Because a sample of larvae captured with a seine and preserved (10% formalin) in 2002 was not measured until 2004, a shrinkage factor of 10.3% was applied to the lengths to adjust for storage in formalin (Marliave, 1980). The left otolith of each fish was cut into thin sections by using standard methods described in the otolith manual for microstructural examination (Secor et al., 1991). The otolith was attached to a glass slide, medial side down, with thermal resin. The surface of the otolith was then ground to the primordium with 1000-grit silicon carbide paper. Care was taken to leave the edge of the otolith intact and not to grind through the primordium in the center. The otolith was then polished with an 8000- and 12,000-grit cloth on both sides to reveal the internal microstructure. Otoliths collected in 2001 were aged separately by two biologists. When age estimates differed, otoliths were re-examined together by both readers, and an age was agreed upon. Otoliths collected in 2002 were aged by one biologist three different times. If age readings differed between any of the three readings, the otolith was re-examined and a best estimate of the age was determined. For both years, otoliths were examined without knowledge of fish size or collection date.

Diet

A sample of Pacific sandfish (>age-0) was preserved in 10% formalin and analyzed for stomach contents. Preserved fish were measured to the nearest mm FL, weighed to the nearest 0.1 g, and stomachs were excised. Stomachs were weighed before and after removal of contents to obtain an estimate of wet weight by subtraction. Contents were examined with a dissecting microscope and identified to major taxonomic groups.

Table 2

Size and age based on surface observations of annual rings on otoliths of Pacific sandfish (*Trichodon trichodon*) from nearshore waters of The Brothers Islands, and from Pybus Bay and Frederick Sound, southeastern Alaska from 2001 to 2003. Fish from Frederick Sound and Pybus Bay were captured with a mid-water trawl, whereas all other fish were captured with a beach seine. Asterisk denotes total length (mm). n = number of sandfish in the sample.

			Fork length (mm)			
Date	Location	n	Mean	Range	Mean weight (g)	Age (yr)
July 2001	The Brothers Islands	22	80	70–95	6.4	1
May 2001	Frederick Sound	1	120	—	24.0	4
May 2001	Frederick Sound	1	190	—	82.0	6
March 2002	The Brothers Islands	9	16*	14–18*	—	0
July 2002	The Brothers Islands	24	70	55–79	4.3	1
July 2002	The Brothers Islands	1	135	—	32.0	5
May 2003	Pybus Bay	1	121	—	23.5	4
May 2003	Pybus Bay	10	141	129–152	37.2	5
May 2003	Pybus Bay	7	160	156–166	58.3	6

Frequency of occurrence (% FO) was determined for each taxonomic group based on the percentage of stomachs in which that taxonomic group occurred. Percent volume (% Vol) of each taxonomic group was estimated visually and total weights per taxon were estimated by multiplying the percent volume by the total stomach weight.

Results

Fish catch and habitat

Total catch of Pacific sandfish was 15,431 fish. Most (99%) fish were captured with a seine: 1027 fish in July (total for all years) and 14,231 larvae in March (total for all years; Table 1). Total trawl catch was 173 fish; 2 fish in Frederick Sound in May 2001 and 171 fish in Pybus Bay in May 2003.

Most Pacific sandfish captured with a seine in July and March each year were found adjacent to steep bedrock outcroppings with attached kelp (Table 1). Water temperatures in summer and winter for all years were about 10°C and 4°C, and salinity ranged from 30 to 33 PSS. Larvae were captured in March at many of the same sites where juveniles were captured in July (sites 1, 9–11, 14; Table 1; Fig. 2). The few adult Pacific sandfish (>130 mm FL) captured with a seine in July 2002 and 2003 were found exclusively in low gradient, sandy habitat (site 1; Fig. 2). Most adult Pacific sandfish were captured in Pybus Bay with a trawl at least 400 m offshore of any land mass and at depths between 14 and 64 m; at the depth (50 m) most fish were captured, temperature was 6.5°C and salinity was 31.5 PSS.

Age and size

Nearly all Pacific sandfish captured with a seine in July (all years) were juveniles; only larvae were captured in March (all years). Approximately 14,000 Pacific sandfish larvae were captured in March (Table 1); mean TL was 16.2 mm (13.1 to 23.2 mm; Fig. 3). Of nine larvae aged from March 2002, all were age-0 (Table 2). Mean FL of Pacific sandfish captured with a seine in July was 86 mm (62 to 150 mm; Fig. 3). Of 47 Pacific sandfish aged from seine catches in July, 46 were age-1 (mean FL=75 mm) and one was age-5 (FL=135 mm) (Table 2).

All trawl-caught Pacific sandfish were adults or subadults. Mean FL of Pacific sandfish from trawl catches was 150 mm (120 to 190 mm; Fig. 3). The 21 fish aged from trawl catches in May (both years) were age-4, age-5, and age-6 (mean FL=121, 141, and 164 mm) (Table 2). No age-2 or age-3 fish were captured in trawls.

Diet

From analysis of 195 stomachs, we found that Pacific sandfish were both planktivorous and piscivorous. Percent weight of stomach contents for age-1 Pacific sandfish varied between years (Fig. 4). For both 2001 and 2002 combined, decapods, fish, and euphausiids accounted for about 90% of stomach content weight. Fish made up 50% of the weight in 2001, but only 7% in 2002. The other two heaviest items, decapods and euphausiids, ranged from 30% to 50% and from 17% to 25% of the weight in 2001 and 2002, respectively. Diet of adult Pacific sandfish (2003; ≥age-4) consisted of four food items and was dominated by fish and decapods (Fig. 4). Fish accounted for 75% of the weight of stomach contents for ≥age-4 fish. Frequency of occur-

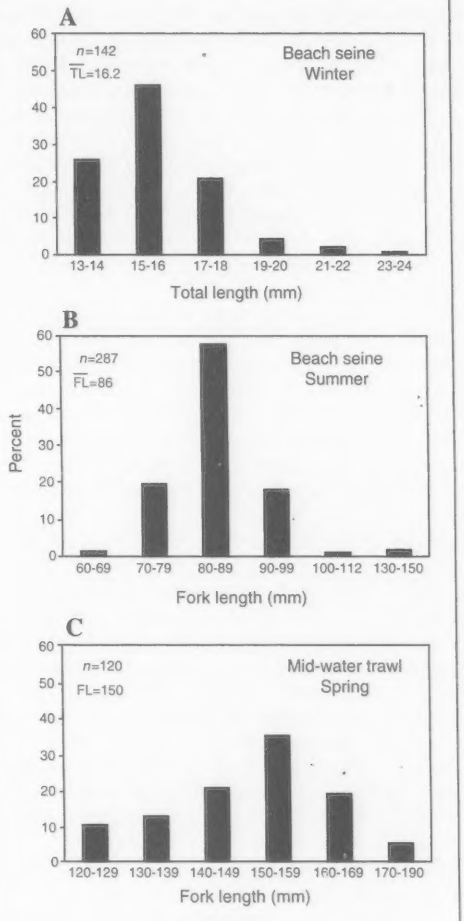

Figure 3

Length frequency of Pacific sandfish (*Trichodon trichodon*) near The Brothers Islands, southeastern Alaska. (**A**) Larvae were captured in March, 2002–2004, (**B**) juveniles and subadults were captured in July, 2001–2003, and (**C**) subadults and adults were captured in May 2001 and May 2003. Total length was measured for larvae and fork length for juveniles, subadults, and adults.

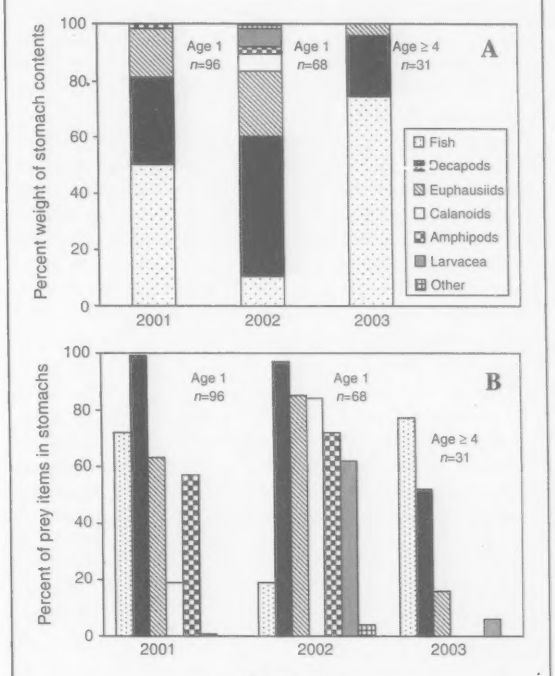

Figure 4

(**A**) Percent weight of stomach contents and (**B**) percent frequency of occurrence of prey items in stomachs of Pacific sandfish (*Trichodon trichodon*) near The Brothers Islands, southeastern Alaska. Data for 2001 and 2002 represent age-1 fish captured with a beach seine in July, and data for 2003 represent fish ≥age 4 captured with a mid-water trawl in Pybus Bay and Frederick Sound in May. See Figure 2 for site locations.

rence of food items in stomachs varied among years for age-1 Pacific sandfish (Fig. 4). Occurrence of fish in stomachs of age-1 fish ranged from 72% in 2001 to 19% in 2002, and occurrence of larvacea ranged from 62% in 2001 to 1% in 2002. Nearly all identifiable fish in juvenile stomachs were gadids. For 2001 and 2002 combined, decapod larvae occurred in about 98% of stomachs, euphausiids in 74%, and amphipods in 65%. For adults (2003; ≥age-4), fish were the most frequently occurring food item and were present in 77% of stomachs.

Discussion

Pacific sandfish larvae and juveniles use shallow, nearshore habitats, whereas most adults occupy deeper waters farther from shore. Larvae were similar in size and anatomical features to larvae (0–29 day-old) described by Marliave (1980). Thus, we estimate that the larvae we captured probably hatched between early February and early March—a hatching period similar to that reported by Clemens and Wilby (1967) for British Columbia, Canada, but 1–2 months earlier than hatching dates estimated by Bailey et al. (1983) for northern southeastern Alaska. Pacific sandfish spawn on rocky intertidal shorelines, eggs incubate for about one year, and larvae develop in shallow nearshore areas (Marliave, 1980). Because of the relative high abundance of Pacific

sandfish larvae in the shallow nearshore waters of The Brothers Islands, this area appears to be an important spawning and nursery area for Pacific sandfish. The length of time that larvae remain in shallow nearshore areas, however, appears to be limited because we captured no age-0 fish in July.

Pacific sandfish have been caught incidentally in a variety of habitats in Alaska. In southeastern Alaska, Orsi and Landingham (1985) caught Pacific sandfish in low-gradient beaches composed of sand, gravel, cobble, or a combination of these substrates, and Orsi et al. (2000) caught Pacific sandfish with a rope trawl in deeper waters. In the Aleutian Islands, Isakson et al. (1971) reported that Pacific sandfish were a prominent species in the inshore sand and gravel community. Pacific sandfish are known to burrow into soft substrates, but most of the juveniles that we captured were close to shore and adjacent to bedrock outcroppings—area and substrate similar to those observed by Bailey et al. (1983). Although Mecklenburg (2003) reported that Pacific sandfish generally burrow in sand during the day and are active at night, we observed large schools of juvenile Pacific sandfish actively feeding near the surface during the day.

Age of Pacific sandfish varied with time of capture. We captured mostly age-1 Pacific sandfish in July; mean size of age-1 fish in our study (75 mm FL) was similar to the size of age-1 fish captured in the northern Gulf of Alaska (71 mm FL; Paul et al., 1997). In spring we captured subadult and adult Pacific sandfish, and in winter we caught only larval Pacific sandfish. Notably absent in all of our catches were age-2 and age-3 fish. Paul et al. (1997) captured age-2 and age-3 Pacific sandfish by a variety of methods in the northern Gulf of Alaska. Most of their sampling, however, occurred in August and in deeper waters (29–55 m). Pacific sandfish may segregate into different habitat types depending on age and size, which may explain the absence of some age classes in our catches.

Diets consisting of crustaceans and fish have been reported for Pacific sandfish similar in size to those in our study (Paul et al., 1997; Sturdevant et al.[2]). Percent FO of fish in the diet of Pacific sandfish was 66% in the Gulf of Alaska (Paul et al., 1997), 100% in Prince William Sound (Sturdevant et al.[2]), and 56% in our study. For crustaceans, the highest % FO was for shrimp (19%) in the Gulf of Alaska (Paul et al., 1997), gammarids (46%) in Prince William Sound (Sturdevant et al.[2]), and crab larvae (83%) in our study. Near Kodiak Island, Alaska, stomach contents of 26 Pacific sandfish in July were dominated by fish (70% by number and 97% by weight; Rogers et al.[3]).

[3] Rogers, D. E., D. J. Rabin, B. J. Rogers, K. Garrison, and M. Wangerin. 1979. Seasonal composition and food web relationships of marine organisms in the nearshore zone of Kodiak Island including ichthyoplankton, meroplankton (shellfish), zooplankton, and fish. Environmental Assessment of the Alaskan Continental Shelf, p. 529–662, vol. IV. Receptors, Fish, Littoral, Benthos. Outer Continental Shelf Environmental Assessment Program, Boulder, CO.

Percent FO of fish in Pacific sandfish stomachs was nearly four times greater in 2001 than in 2002, which probably reflects the abundance of prey. Based on seine catches at The Brothers Islands, the relative abundance of young-of-the-year (YOY) gadids, the dominant fish identified in Pacific sandfish stomachs, was over six times greater in 2001 than in 2002 (Thedinga et al., 2006). In addition, mean length of Pacific sandfish was about 5 mm longer in 2001 than in 2002, which may reflect the increased presence of fish in the diet of Pacific sandfish, or could be due to increased growth time because we sampled 10 days later in 2001 than in 2002.

Diet differed by fish size. Larger Pacific sandfish (mean FL 150 mm) ate mostly fish, whereas smaller Pacific sandfish (mean FL 86 mm) ate mostly decapods. Paul et al. (1997) also observed a change in diet based on fish size; % FO of fish in the diet of Pacific sandfish greater than 115 mm FL was 90% compared to 14% for fish less than 99 mm. Also in their study, mean % FO of non-fish food items was 5% for larger fish compared to 24% for smaller fish.

Bailey et al. (1983) reported observing juvenile Pacific sandfish in mixed schools with pink salmon (*Oncorhynchus gorbuscha*) fry, but we caught Pacific sandfish with YOY walleye pollock (*Theragra chalcogramma*), YOY Pacific cod (*Gadus macrocephalus*), YOY Pacific herring (*Clupea pallasii*), and juvenile chum salmon (*Oncorhynchus keta*). Apparently, Pacific sandfish exhibit schooling behavior as larvae and juveniles and co-occur with a variety of forage species, sometimes preying on those that are of consumable size. High predation rates of juvenile walleye pollock by Pacific sandfish have been reported for the Bering Sea and Gulf of Alaska (Guénette, 2005).

Shallow nearshore waters provide important nursery and spawning habitat for Pacific sandfish. Pacific sandfish diet varied between size classes and years which was probably dependent on abundance of YOY walleye pollock. Pacific sandfish are a nutritious forage fish with moderately high oil, protein, and caloric content (Anthony et al., 2000; Logerwell and Schaufler, 2005) and could therefore be important to some predators at certain times of the year. For example, Pacific sandfish occurred in up to 64% of Steller sea lion (*Eumetopias jubatus*) scats in the Aleutian Islands (Sinclair and Zeppelin, 2002). The dependence of Pacific sandfish upon nearshore areas for spawning, egg incubation, and larval rearing, coupled with the greater sensitivity to pollutants of early life stages than adults (Carls et al., 1999), warrant the protection of nearshore areas from shoreline development and pollutants to maintain healthy forage fish populations.

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Genetic diversity of yellow grouper (*Epinephelus awoara*) determined by random amplified polymorphic DNA (RAPD) analysis

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The development of molecular techniques has enhanced our ability to identify fish species. A few molecular markers, such as mitochondrial DNA and ribosomal DNA, have been used to assist in the identification of fish species. One such technique now routinely used is the random amplified polymorphic DNA polymerase chain reaction (RAPD-PCR; Williams et al., 1990). Genetic analysis with RAPD markers is relatively easy, fast, and efficient. RAPD analysis, however, may not be practical for identifing species that interbreed (Martinez et al., 1997). Although the major limitation of RAPD technique for identification of intraspecific specimens is its repeatability, adherence to protocol and standardized reactions can improve the method (Jones et al., 1997). This technique has been used for identification and detection of genetic diversity in various fish species (tilapia; Naish et al., 1995; striped bass; Bielawski and Pumo, 1997; grouper; Asensio et al., 2002). Most other DNA-based methods are more laborious and time consuming than RAPD, making them less suitable for large population or genetic diversity studies. Suitable loci with high reproducibility allow the identification of unequivocally distinct species (i.e., where there is large genetic differentiation between species, compared to within species; Greig et al., 2005).

Groupers (Epinephelinae: Serranidae) are among the most important and highly valued demersal species of tropical and subtropical coastal areas worldwide. In general, grouper species lack distinct morphological specializations, but color patterns and geographic location are used in the field. Some confusion exists over the names of some important Indo-Pacific grouper species (Heemstra and Randall, 1993; Sadovy, 1997) and little work has been done to establish species identities and their genetic diversity. One alternative to gathering information on these species is the use of molecular genetic markers. In the present study, RAPD analysis has been used to investigate the genetic variation in two populations of yellow grouper (*Epinephelus awoara*) from the South China Sea.

Materials and methods

Sample preparation and DNA extraction

Yellow grouper were obtained from two populations (30 individuals from Xiamen and 26 individuals from Guangdong) of the South China Sea. Muscle samples from fish were taken, placed in 95% ethanol, transported to the laboratory, and stored at −20°C until analysis. Genomic DNA was extracted according to the DNA extraction method of DeSalle et al. (1993).

Primer selection and RAPD reaction profile

Twenty primers (Table 1) were selected on the basis of presence of intense, well-distinguished, and reproducible bands for further analysis. PCRs for each population were performed in 2-μL volumes containing 100 mM Tris-HCl (pH 8.3), 500 mM KCl, 15 mM $MgCl_2$, 1 μL dNTPs, 0.4 unit rTaq polymerase and approximately 20 ng of template DNA and 1 μL of each primer. Thermocycling conditions were as follows: initial denaturation step of 95°C for 5 min., 30 cycles of 45 s at 93°C, annealing temperature of 45 s, primary extension of 72°C for 2 min., and a final extension of 72°C for 5 minutes.

Detection of amplified DNA

Electrophoresis of a 10-μL portion of the amplification reaction was performed for 45 minutes at 100 V in a 1.2 % agarose gel containing ethidium bromide (1 μg/mL) in Tris-acetate buffer (0.004 M Tris acetate, 0.001 M EDTA, pH 8.0). DNA fragments were viewed with UV transillumination and analyzed with Genescan (Gene-Geneius Bio-imaging System, Cambridge, England). Their sizes were estimated by comparison with a commercial 1-kb plus DNA ladder.

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Table 1

Primer details and pattern of polymorphism in two sampled populations (Xiamen and Guangdong) of *Epinephelus awoara*. SN=serial number. XM = Xiamen; GD = Guangdong.

SN	Primers	DNA sequence	No. of bands	Total no. of polymorphic loci	Polymorphic loci in the two populations		Percentage of polymorphic loci
					XM	GD	
1	S117	CACTCTCCTC	8	7	7	4	87.5
2	S465	CCCCGGTAAC	9	8	8	2	88.9
3	S513	GGACGACAAG	6	5	0	5	83.4
4	S514	CAGGATTCCC	9	5	5	4	55.6
5	S515	GGACAACGAG	7	5	5	3	71.4
6	S517	CCGTACGTAG	10	10	10	5	100.0
7	S520	ACGGCAAGGA	7	6	6	6	85.71
8	S1021	GGCATCGGCT	10	7	7	3	70.0
9	S1023	GGGTCCAAAG	8	7	2	7	87.5
10	S1026	TGCCGCACTT	8	8	8	1	100.0
11	S1036	AAGGCACGAG	10	6	6	5	60.0
12	S1037	CCTCACGTCC	7	5	5	1	71.4
13	S1040	CCTGTTCCCT	10	7	7	2	70.0
14	S1042	TCGCACAGTC	6	2	2	2	33.3
15	S1043	AGCACCTCGT	11	11	11	6	100.0
16	S1044	GAATGCGACC	7	5	5	1	71.4
17	S1045	CAGCGTTGCC	10	7	5	7	70.0
18	S1049	ACGGCACGCA	5	3	3	3	60.0
19	S1053	CAGCCGTTCC	6	4	1	4	66.7
20	S1055	GAATCCGGCA	5	3	3	3	60.0
	Total			159	121	106	74
	Percentage of polymorphic loci			76.10	66.66	46.54	

Data analysis

The presence (1) or absence (0) of RAPD products was scored for all loci based on a minimum of two replicates. Only those characters that could be reliably scored from replicate RAPD reactions were included in the analysis. Loci that failed to generate RAPD amplification products were excluded from the analysis. Probability (Fischer's exact test) was carried out to evaluate differences in homogeneity of gene frequencies across populations for each loci. Test of heterozygosity (H_T), expected heterozygosity (H_S), population differentiation (G_{ST}), and gene flow (N_m) were also conducted between two populations of *Epinephelus awoara*.

Results

Two populations of *Epinephelus awoara* were analyzed to characterize the RAPD marker for genetic variation.

Useful RAPD primers and markers for genetic variation

The first group of 20 primers (Table 1) produced a total of 159 bands, among which 121 polymorphic bands (76.10%) were observed. The 38 monomorphic bands (23.90%) could be considered, on a preliminary basis, as population diagnostic bands that allow clear differentiation among populations of *Epinephelus awoara* because they were present in all individuals analyzed. Primers S514, S1021, S1036, S1040 and S1042 generated more diagnostic bands than did other primers. The absence of these markers in related populations must, however, still be confirmed.

Primers that showed high levels of reproducibility also produced more polymorphic bands. Over five polymorphic bands (5.76) per primer were produced from 20 primers on average. All 20 primers (Table 1) yielded satisfactory amplification products for all specimens tested. Each primer produced a unique band pattern of amplified DNA. For a given primer and DNA template, a number of bands appeared intense and reproducible in all the replicates, and bands of weaker stain appeared occasionally. All primers were able to distinguish two populations of *E. awoara*, reproducing different and well-characterized banding patterns. Banding pattern variations observed with some primers were not consistent for all individuals within or between populations and therefore these variations should be attributed to intraspecific polymorphism.

High rates of RAPD polymorphism

Polymorphic rates of RAPD bands were much higher between two populations of *Epinephelus awoara*. The number of reproducible and well-resolved bands analyzed in the two populations ranged from 5 to 11. Monomorphic bands, constantly present in all individuals, varied between primers, whereas total polymorphic bands were observed 76.10% of the time for the two populations of *E. awoara*. The Xiamen population of *E. awoara* exhibited 66.66% polymorphism, whereas polymorphism was 46.54% in the Guangdong population (Table 1). RAPD fragments of fewer than 1000 base pairs were found to be more polymorphic than larger fragments.

Genetic diversity

Genetic diversity between populations was clearly illustrated in Table 2 and Table 3. The genetic diversity statistics (H_T, H_S, G_{ST}, N_m) estimated between the two populations of *Epinephelus awoara* for each primer are listed in Table 3. Nei's (1973) unbiased measures of genetic identity and genetic distance between two populations were 0.6216 and 0.4755, respectively. Within the populations, total heterozygosity varied from 0.2189 to 0.4616 and expected heterozygosity ranged between 0.1232 and 0.2920. Probability (Fisher's exact test) of homogeneity was significant at $P>0.05$ for all primers except S465, S513, S1026, S1044, and S1055.

Discussion

This study showed a considerable amount of genetic variation present in *Epinephelus awoara*. RAPD analysis generated a large number of polymorphic DNA bands (Table 1) between the populations of *E. awoara*, thus making it one of the most efficient systems for generating DNA markers. However, low levels of interspecific variation were found in RAPD profiles among strains of grouper. Therefore, it was an inefficient system for generating molecular markers for gene mapping (Liu et al., 1999).

Several authors (Welsh and McClelland, 1990; Bardakci and Skibinski, 1994; Naish et al., 1995) have demonstrated that the RAPD PCR method is a powerful tool for the assessment of genetic markers that are capable of discriminating between species or subspecies in a wide range of organisms, including fishes. This capacity was confirmed by the results of the present study because, for all screened primers, different RAPD banding patterns were observed between the two populations (Table 1). A limitation arising with the application of the RAPD technique is the homology between comigrating bands produced by the same primer in different individuals (Hadrys et al., 1992). Nevertheless, in the present study, homology constitutes a valid assumption because all individuals belong to the same species.

Despite the fact that no specific markers were found to identify *Epinephelus awoara* species, data analysis of the observed and effective number of alleles revealed a degree of divergence (Table 2). The Nei (1973) gene diversity was also illustrated in Table 2. The two populations of *E. awoara* (Table 3) showed high level of genetic variation (i.e., Shannon's information index; Shannon-Weaver, 1949, average genetic index [H_{POP}] and genetic diversity index between populations [H_{SP}]). Similarly a high level of genetic variation and genetic distance (0.617–0.949) was observed in dinoflagellates (Baillie et al., 2000). This finding supports a high genetic distance for *E. awoara* (0.4755) in the present study. This may be due to the selection pressure of pollutants (Nadig et al., 1998) or to overexploitation of groupers in the South China Sea.

Total heterozygosity (H_T) values ranged from 0.2189 to 0.4616, expected heterozygosity (H_S) from 0.1232 to 0.3157, and an estimate of gene flow (N_m) from 0.3714 to 4.1722. The proportion of total genetic variation within species due to population differentiation (G_{ST}) ranged from 0.1070 to 0.5344 (Table 3). Carvalho et al. (1991) observed a very high differentiation (G_{ST}=0.648) in the guppy (*Poecilia reticulata*) in northern Trinidad. Similarly, Ward et al. (1994) also observed high G_{ST} values (>0.2000). In any case, the divergence in G_{ST} values indicates that, on average, marine subpopulations exchange between one and two orders of magnitude more migrants per generation. Genetic divergence between areas originates when populations are formed or through the restriction of gene flow (Lage et al., 2004). Higher H_S in marine fish is at least consistent with these fish having, on average, larger population sizes. Homogeneity of gene frequencies was found to be significant ($P>0.05$) across populations of *Epinephelus awoara* (Fig. 1) for most of the primers except S465, S513, S1026, S1044,and S1055 ($P>0.001$).

The factor that could influence the genetic variation of the grouper population geographically is the movement of adults, which can be extensive and cover considerable distances (Harding et al., 1997). The otherwise shelter-habituated adults travel long distances necessary to populate remote oceanic islands. The Bermuda fauna include more than 75% of the known west Indian groupers even though Bermuda lies more than 800 miles from other coral reefs. Such distributional patterns are best explained as the result of passive transport of larvae by oceanic currents. Similar patterns are also expected in the South China Sea. Adult movement of marine fish is relatively unfettered by physical barriers. In addition to gene flow through adult migration, marine fish frequently have a planktonic larval stage of several months duration, which can be expected to further enhance gene flow.

Estimation of genetic diversity of *Epinephelus awoara* by RAPD analysis (i.e., by using the mean of observed number of alleles [*Na*], effective number of alleles [*Ne*] and Nei's gene diversity [*H*]) was found to be 1.6563, 1.4169, and 0.2915, respectively for Xiamen populations, whereas they were 1.4824, 1.2713, 0.2167, respectively for Guangdong populations. Our results provide evidence for a loss (10.5%, 11.3%, and 25.7%, respec-

Table 2

Genetic variation in two sampled populations (Xiamen and Guangdong) of *Epinephelus awoara*. Na = Observed number of alleles; *Ne* = Effective number of alleles; *H* = Nei's (1973) gene diversity; *Ho* (I) = observed heterozygosity (Shannon's information index).

	Na		*Ne*		*H*		*Ho* (I)	
Loci	Xiamen	Guangdong	Xiamen	Guangdong	Xiamen	Guangdong	Xiamen	Guangdong
S117	1.8750	1.5000	1.5318	1.2272	0.3145	0.1449	0.4675	0.2254
S465	1.8889	1.1111	1.6659	1.0927	0.3673	0.0505	0.5324	0.0719
S513	1.0000	1.8333	1.0000	1.5851	0.0000	0.3298	0.0000	0.4819
S514	1.5556	1.4444	1.3886	1.1905	0.2231	0.1310	0.3269	0.2074
S515	1.7142	1.4285	1.2984	1.1368	0.1924	0.1019	0.3076	0.1565
S517	2.0000	1.5000	1.6602	1.2678	0.3886	1.1696	0.5808	0.2593
S520	1.7142	1.8571	1.5315	1.5871	0.2877	0.3580	0.4162	0.5048
S1021	1.8000	1.3000	1.3246	1.1497	0.1959	0.0946	0.3077	0.1463
S1023	1.2500	1.8750	1.1780	1.4712	0.1004	0.3229	0.1469	0.4806
S1026	2.0000	1.1250	1.6661	1.0575	0.3859	0.0394	0.5691	0.0618
S1036	1.7000	1.4000	1.3534	1.3771	0.3038	0.1940	0.2334	0.2712
S1037	1.7142	1.1428	1.4307	1.0318	0.2254	0.0260	0.3769	0.1039
S1040	1.7000	1.2000	1.5307	1.0605	0.3011	0.0464	0.4348	0.0786
S1042	1.3333	1.3333	1.2429	1.1814	0.1358	0.1107	0.1945	0.1689
S1043	2.0000	1.4545	1.7466	1.1649	0.4081	0.1044	0.5911	0.1694
S1044	1.7142	1.1428	1.4483	1.0057	0.2689	0.0054	0.3997	0.0136
S1045	1.5000	1.8000	1.4107	1.5349	0.2189	0.3146	0.3126	0.4642
S1049	1.6000	1.6000	1.5417	1.3333	0.2839	0.2124	0.3994	0.3228
S1053	1.6666	2.0000	1.1519	1.4657	0.0795	0.3059	0.1116	0.4780
S1055	1.4000	1.6000	1.2359	1.5058	1.1478	0.2722	0.2223	0.3871
Mean	1.6563	1.4824	1.4169	1.2713	0.2915	0.2167	0.3466	0.2527

tively for *Na*, *Ne*, and *H*) of genetic diversity; this loss may be due to high fishing pressure of the grouper population in Guangdong.

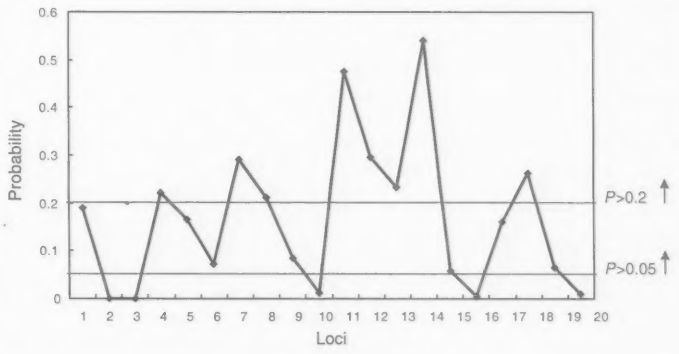

Figure 1

Probabilities ($P>0.05$) that show the significance of homogeneity of gene frequencies across populations of yellow grouper (*Epinephelus awoara*). Arrows show the range of probability.

Conclusion

These results indicate that commercial fishing may result not only in selective genetic changes in exploited stocks but also in reduced genetic diversity due to genetic drift. The loss of genetic diversity may be particularly pronounced during the initial stages of exploitation, and investigations into the advanced stages of exploitation may be less likely to detect significant changes in allelic diversity. This loss can also be tested for other commercially exploited species of grouper in genetic and demographic context. In the present study, the RAPD method proved useful and technically convenient for the study of genetic diversity of yellow grouper (*Epinephelus awoara*); therefore, it can also be applied to other species of grouper and enable the analysis of many samples in a short time. The present work also indicates that molecular markers used

in present study are a practical approach for studies of genetic diversity

Acknowledgments

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Improving the precision of otolith-based age estimates for Greenland halibut (*Reinhardtius hippoglossoides*) with preparation methods adapted for fragile sagittae

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Otolith-based age estimates for Greenland halibut (*Reinhardtius hippoglossoides*) have low precision, and there is general uncertainty about their accuracy in older fish (Anon.[1]; Alpoim et al.[2]). Low precision can result from inadequate training of age readers, poor aging criteria, or peculiarities of the structure being aged (Kimura and Lyons, 1991). The latter is the primary cause of low precision with Greenland halibut, and it confounds attempts to improve the former two. Sagittae of Greenland halibut are irregular in shape and exhibit marked bilateral asymmetry (Fig. 1). Much of this irregularity is due to finger-like projections, which begin as small, marginal tubercles in 4- to 6-year-old fish, and can develop into convoluted, fragile structures in older fish. The variable deposition rate of aragonite and protein that produces these structures makes interpretation of growth patterns difficult and results in age estimates that vary depending on which region of the otolith is examined.

The amphiboreal distribution of Greenland halibut has led to their exploitation by the industrial fisheries of more than ten nations in the North Atlantic and North Pacific Oceans and by several aboriginal fisheries in the near shore regions of Greenland and northern Canada (Alton et al., 1988; Witherell[3]; Anon.[4]; Treble[5]). Age determination (aging) and age structure analysis have been undertaken primarily for North Atlantic and Barents Sea stocks. Methods vary between laboratories but the majority of aging is accomplished by examining the surface patterns of whole sagittae. For the purposes of this note, "surface" (or "surface aging") will refer to the surface pattern of the whole sagitta. Generally, only the left (i.e., blind side of fish) sagitta is aged because it has a more centric nucleus, resulting in more evenly spaced annuli (Lear and Pitt, 1975; Bowering, 1978, 1982; Haug and Gulliksen, 1982; Anon.[1]; Bowering and Nedreaas, 2001; Alpoim et al.[2]). Attempts to improve the resolution of growth patterns have included baking both sagittae, clearing them with oil, grinding the distal surface of the left sagitta, and breaking and burning the left sagitta (Anon.[1]; Kuznetsova et al., 2001; Alpoim et al.[2]). To date these processes have had equivocal effects on the precision of age estimates. International exchanges of Greenland halibut otoliths have yielded mixed results; reported between-reader agreement (±0 year) has ranged from 1% to 69% (Anon.[1]) and from 37% to 51% (CVs ranging from 5.81% to 9.58%) (Alpoim et al.[2]). Despite these exchanges, concern about precision still exists and a consensus on preferred aging methods for Greenland halibut has not been reached.

The Alaska Fisheries Science Center (AFSC) has collected Greenland halibut otoliths from the Bering Sea and Aleutian Islands for over 20 years, but little aging was attempted prior to 2003. Initial examination of the otoliths left AFSC age readers

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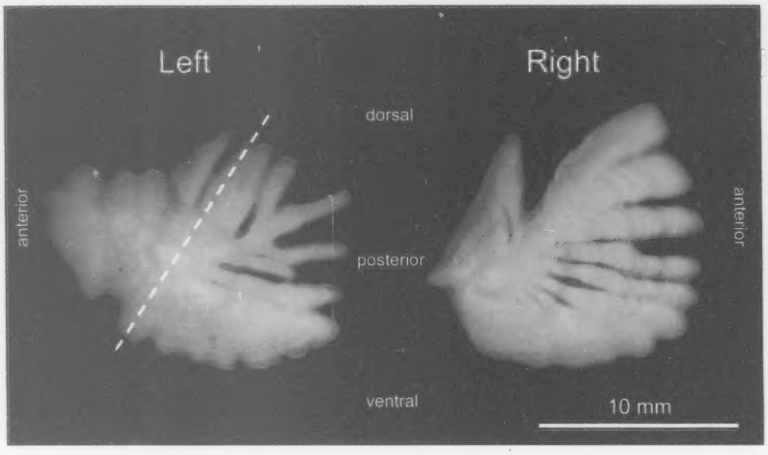


Figure 1

Micrograph of sagittae from a 92-cm Greenland halibut (*Reinhardtius hippoglossoides*). View is of the distal surface. Dashed line indicates the plane of the cross section used in this study.

with a general lack of confidence in surface age estimates. This uncertainty, coupled with the observation that otoliths of larger, presumably older, fish tend to grow in thickness rather than in sagittal diameter, led to pilot work for processing and production (large-scale) aging of Greenland halibut sagittae. Various methods reported in the literature and several new techniques were explored. This pilot work converged on a method that involved cutting the left sagitta in the transverse plane and staining the two restulting cross sections. This method is similar to the break-and-burn method (Chilton and Beamish, 1982) but is more amenable to fragile Greenland halibut sagittae. The goal of the present study was to determine whether the precision of Greenland halibut age estimates could be improved by examining the stained cross sections of their sagittae rather than the surfaces of the whole sagittae, and to determine whether there was a significant difference in age estimates made with each of the two methods.

Materials and methods

Otoliths were collected from Greenland halibut in July 1998 and June–August 1994 as part of the AFSC Bering Sea and Aleutian Islands trawl surveys. Sagittae were removed at sea and stored in a glycerol-thymol solution until the time of our study. Fish length (TL) was measured to the nearest centimeter for each specimen.

Surface aging was accomplished by submerging sagittae in water over a black background and counting probable annuli (i.e., translucent zones) with a dissecting microscope (6–25×) with reflected light. Probable annuli were counted along several vectors on both sides of the right and left sagittae. A count that was repeatable, with highest reader confidence, was adopted as the surface age estimate.

The left sagitta (i.e., on blind side of fish) was embedded in clear polyester resin and cut into two pieces with a low-speed saw. The cut was made slightly obliquely to the transverse plane and was adjusted for each otolith to ensure that the saw blade bisected the nucleus, passed through a thick section of the perisulcular region (i.e., a portion with a large mediolateral dimension), and extended out the center of a prominent dorsal finger (Fig. 1). The two exposed cross sections were then polished with 800-grit wet-dry sandpaper on a lapidary wheel to remove saw marks.

Staining techniques were adapted from Richter and McDermott (1990). Polyester blocks containing cut otoliths were submerged in a solution of 1% Aniline Blue WS (no. B362-03, Mallinckrodt Baker Inc., Phillipsburg, NJ) in 1% acetic acid. Staining times varied from 10 to 15 minutes initially and were consolidated to 13 minutes as the experiment progressed. Stain solution temperature was maintained between 20° and 23°C. Upon removal from the stain, otoliths were rinsed with fresh water and wiped clean to ensure that residual acid and stain were removed. The two cross sections were covered with mineral oil to eliminate glare, and were examined under a dissecting microscope at 12× to 50× magnification with reflected light. Blue stained translucent zones (Fig. 2) were counted, and this number was adopted as the cross-section age estimate.

Three trials were conducted to examine the possible benefits of cutting and staining Greenland halibut sagit-

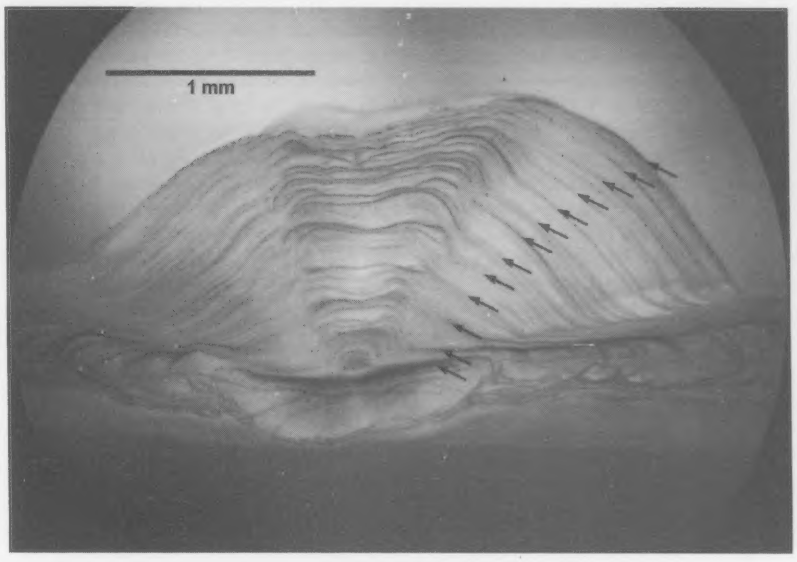


Figure 2

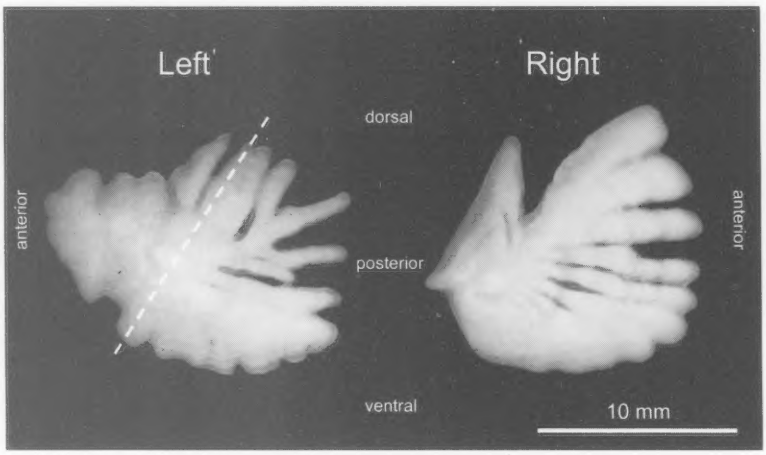
Stained cross section of the left sagitta from an 84-cm Greenland halibut (*Reinhardtius hippoglossoides*). Arrows point to presumed annual marks in the perisulcular tuberosity where annuli were most readily resolved. Fish age was estimated at 13 years.

tae. In trial 1, a training trial, sagittae of 93 Greenland halibut were examined to compare precision between the two aging methods and to calibrate age readers with respect to the first few annuli on the stained cross sections. This sample included fish that ranged from 12 to 84 cm TL, but it was dominated by smaller fish (mean TL=40 cm, median=31 cm). Two readers independently aged sagittal surfaces and stained cross sections. Surface aging necessarily preceded cutting and staining, but no consultation occurred between readers until the end of the trial. Readers were aware of fish length during aging. At the end of trial 1 the independently determined age estimates were compared and readers re-examined otoliths that had resulted in age discrepancies.

In trial 2, 226 otolith pairs were examined. This sample contained sagittae from many larger specimens (mean TL=75 cm, median=72 cm, and range=57 to 98 cm). Ages were determined in the same manner as in trial 1. However, after surface aging, readers re-examined discrepancies together and assigned, by mutual agreement, a definitive surface age to each sagitta prior to cutting and staining. Similarly, the cross sections were aged independently and then assigned a definitive cross-section age by mutual agreement. This process is similar to that used for production aging of other species at the AFSC (Kimura and Lyons, 1991) and allowed not only a comparison of precision between methods but also a comparison of the final age estimates that resulted from the two methods. In trial 3, sagittae were examined from 76 Greenland halibut with a size range of 12 to 63 cm TL (mean=37 cm, median=39 cm). This trial was conducted in the same manner as trial 2, with the exception that fish length was not provided to the readers. We felt that criticism could arise if length data were known because of the potential for reader bias when aging small fish that fall into distinct size classes.

Two age readers performed each trial. Reader 1 was relatively inexperienced with six months of experience aging larval otoliths and one month of experience aging adult otoliths. Reader 2 had 14 years of experience aging several species, including other Bering Sea flatfishes. Neither reader had previously aged Greenland halibut.

Between-reader agreement and coefficient of variation (CV) were calculated for each aging method from each trial. CV was used as the measure of precision (Chang, 1982). Percent agreement is not a good measure of precision because it is highly dependent on the age structure of the sample. Bowker's test of symmetry (Hoenig et al., 1995) was used to assess between-reader bias. Definitive ages from trials 2 and 3 were compared by using a two-tailed matched pairs *t*-test (Snedecor and Cochran, 1967). Von Bertalanffy growth parameters were estimated from surface and cross-section ages combined from trials 2 and 3. An *F*-test based on the residuals of nonlinear least-squares fit was used to test for difference between the resulting models (Quinn and Deriso, 1999).



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Staining techniques were adapted from Richter and McDermott (1990). Polyester blocks containing cut otoliths were submerged in a solution of 1% Aniline Blue WS (no. B362-03, Mallinckrodt Baker Inc., Phillipsburg, NJ) in 1% acetic acid. Staining times varied from 10 to 15 minutes initially and were consolidated to 13 minutes as the experiment progressed. Stain solution temperature was maintained between 20° and 23°C. Upon removal from the stain, otoliths were rinsed with fresh water and wiped clean to ensure that residual acid and stain were removed. The two cross sections were covered with mineral oil to eliminate glare, and were examined under a dissecting microscope at 12× to 50× magnification with reflected light. Blue stained translucent zones (Fig. 2) were counted, and this number was adopted as the cross-section age estimate.

Three trials were conducted to examine the possible benefits of cutting and staining Greenland halibut sagit-

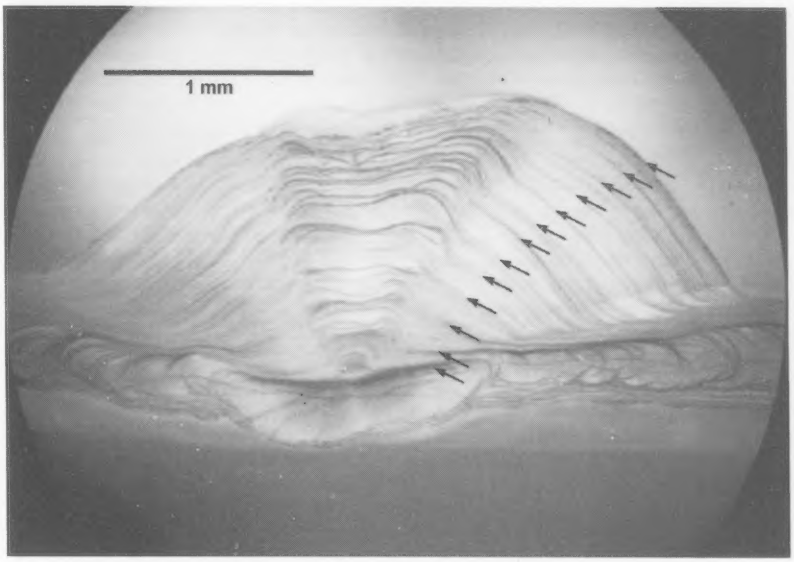

Figure 2

Stained cross section of the left sagitta from an 84-cm Greenland halibut (*Reinhardtius hippoglossoides*). Arrows point to presumed annual marks in the perisulcular tuberosity where annuli were most readily resolved. Fish age was estimated at 13 years.

tae. In trial 1, a training trial, sagittae of 93 Greenland halibut were examined to compare precision between the two aging methods and to calibrate age readers with respect to the first few annuli on the stained cross sections. This sample included fish that ranged from 12 to 84 cm TL, but it was dominated by smaller fish (mean TL=40 cm, median=31 cm). Two readers independently aged sagittal surfaces and stained cross sections. Surface aging necessarily preceded cutting and staining, but no consultation occurred between readers until the end of the trial. Readers were aware of fish length during aging. At the end of trial 1 the independently determined age estimates were compared and readers re-examined otoliths that had resulted in age discrepancies.

In trial 2, 226 otolith pairs were examined. This sample contained sagittae from many larger specimens (mean TL=75 cm, median=72 cm, and range=57 to 98 cm). Ages were determined in the same manner as in trial 1. However, after surface aging, readers re-examined discrepancies together and assigned, by mutual agreement, a definitive surface age to each sagitta prior to cutting and staining. Similarly, the cross sections were aged independently and then assigned a definitive cross-section age by mutual agreement. This process is similar to that used for production aging of other species at the AFSC (Kimura and Lyons, 1991) and allowed not only a comparison of precision between methods but also a comparison of the final age estimates that resulted from the two methods. In trial 3, sagittae were examined from 76 Greenland halibut with a size range of 12 to 63 cm TL (mean=37 cm, median=39 cm). This trial was conducted in the same manner as trial 2, with the exception that fish length was not provided to the readers. We felt that criticism could arise if length data were known because of the potential for reader bias when aging small fish that fall into distinct size classes.

Two age readers performed each trial. Reader 1 was relatively inexperienced with six months of experience aging larval otoliths and one month of experience aging adult otoliths. Reader 2 had 14 years of experience aging several species, including other Bering Sea flatfishes. Neither reader had previously aged Greenland halibut.

Between-reader agreement and coefficient of variation (CV) were calculated for each aging method from each trial. CV was used as the measure of precision (Chang, 1982). Percent agreement is not a good measure of precision because it is highly dependent on the age structure of the sample. Bowker's test of symmetry (Hoenig et al., 1995) was used to assess between-reader bias. Definitive ages from trials 2 and 3 were compared by using a two-tailed matched pairs *t*-test (Snedecor and Cochran, 1967). Von Bertalanffy growth parameters were estimated from surface and cross-section ages combined from trials 2 and 3. An *F*-test based on the residuals of nonlinear least-squares fit was used to test for difference between the resulting models (Quinn and Deriso, 1999).

Results

Stained cross sections improved the precision of Greenland halibut age estimates for the larger, presumably older, specimens in trial 2 but did not improve precision of estimates for specimens in trials 1 and 3. Percent CVs were 11.33, 16.31, and 8.11 for surface ages and 19.68, 9.64, and 9.96 for cross-section ages from trials 1, 2, and 3, respectively (Table 1). A similar pattern occurred in the symmetry of age estimates. Bowker's test of symmetry indicated that surface age estimates in trial 2 were significantly biased between age readers ($P<0.0342$) and that cross-section estimates were not ($P<0.2159$), whereas in trials 1 and 3 significant bias occurred in the cross-section estimates ($P<0.0001$ and $P<0.0012$, respectively) (Table 1).

These equivocal results were primarily caused by difficulty interpreting the second annuli on cross sections. Reader 1 tended to count a small diameter mark close to the nucleus as the second year whereas reader 2 considered it a check. A *post hoc* correction of this bias in trial 1 (i.e., adding 1 year to each of reader-2's cross-section estimates) yielded better precision (CV=7.68) and no significant bias ($P<0.2440$) (Table 1). This problem in interpretation occurred in all trials but the resulting bias was most noticeable in trials 1 and 3 where fish age estimates were younger.

Definitive cross-section ages were significantly greater (older) than definitive surface ages for trial 2 ($t=17.32$, df = 225, $P<0.0001$). Mean cross-section age was 17.1 years and had a range from 9 to 36 years, whereas mean surface age was 12.4 years and had a range from 7 to 28 years (Fig. 3A). Differences between definitive cross-section ages and definitive surface ages in trial 3 were not significant ($t=1.74$, df=74, $P<0.0858$). Mean stained age was 4.29 years and had a range from 1 to 7 years, and mean surface age was 4.15 years and had a range from 1 to 8 years (Fig. 3B). Von Bertalanffy growth parameters calculated from the definitive surface ages (trial 2 and 3 combined) were $L_\infty=103.7$, $K=0.104$, and $t_0=-0.333$. Parameters from definitive cross-section ages were $L_\infty=86.2$, $K=0.125$, and $t_0=-0.233$. The models varied significantly from each other ($F=40.58$, $P<0.0001$) (Fig. 4).

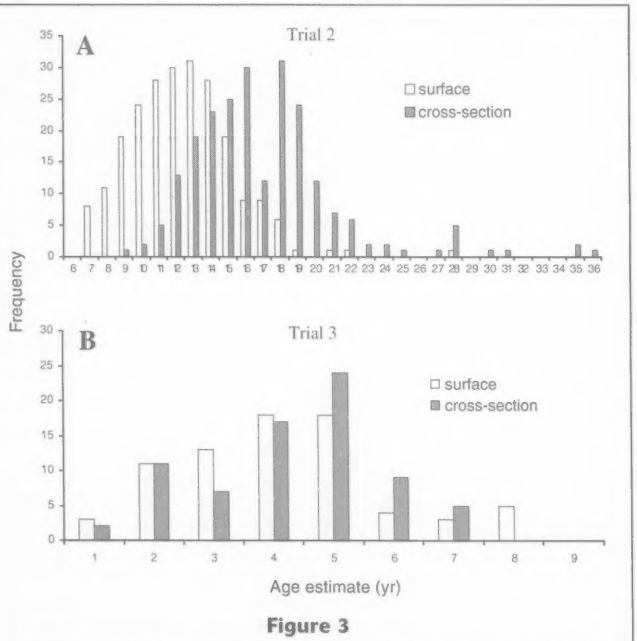

Figure 3

Age frequencies for age estimates from sagittal surfaces and from sagittal cross sections of Greenland halibut (*Reinhardtius hippoglossoides*) in trial 2 (**A**) and trial 3 (**B**) of this study.

Discussion

In larger Greenland halibut (i.e., in trial 2), the precision of age estimates can be improved by aging stained cross sections of sagittae rather than aging sagittal surfaces (Table 1). The sagittae of larger, older Greenland halibut are very difficult to interpret from the surface. Marginal growth increments are very small and are interrupted by the fingerlike projections on the otoliths. Age readers in our study were more confident in the age estimates they made from stained cross sections. The clearest annuli were encountered in the perisulcular region of left sagittae. This region appears to grow more consistently than other areas of the otolith. Staining allowed resolution of very narrow increments in this region that were not visible on the surface of sagittae.

Precision did not increase in trials 1 and 3 (Table 1) because these trials contained many smaller specimens. The benefits of cross-sectioning and staining are not as great in otoliths that are still growing rapidly in sagittal diameter. The magnitude of the difference in age estimates from whole surfaces and stained cross sections did not exceed 1 year in fish less than 46 cm and did not exceed 2 years in fish less than 57 cm. A second confounding factor was interpretation of the second annuli in cross sections. This consistent one-year bias between readers outweighed any improvements that may have resulted from cross-sectioning otoliths in smaller specimens. We feel that more interreader calibration and validation of cross-sectioned annuli by the Peterson method (Ricker, 1975) can resolve this problem.

The increase in precision in trial 2 was accompanied by age estimates that were significantly greater (older) (Fig. 3A). In 24 cases, the cross-section estimate was 10 or more years greater than the surface age estimate, and in two cases the cross-section estimate was 22 years greater. The mean

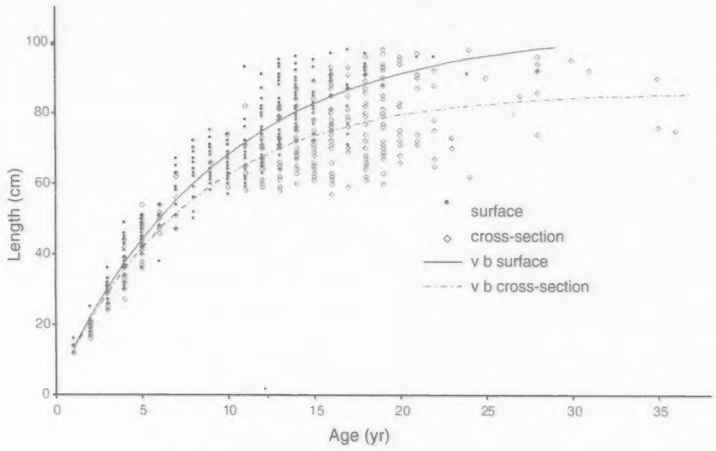

Figure 4

A comparison of plots of length at age for surface ages and cross-section ages of Greenland halibut (*Reinhardtius hippoglossoides*). Von Bertalanffy (vb) growth curve fits for surface aging (solid line) and cross-section aging (dashed line) are shown.

Table 1

Precision of age estimates made from the surfaces and cross-sections of Greenland halibut (*Reinhardtius hippoglossoides*) sagittae. Data from three trials with mean fish length and collection location indicated. BS = Bering Sea, AI = Aleutian Islands.

		Collection year, location	Mean fish length (cm)			Between reader % agreement			Bowker's test of symmetry[2]		
	n			Ageing method	Percent CV[1]	±0 yr	±1 yr	±2 yr	χ^2	df	*P*<
Trial 1	93	1998, BS	40	surface	11.33	44.1	81.7	90.3	30.4	22	0.1091
				cross-section	19.68	20.4	66.7	81.7	74.0	28	0.0001
				cross-section corrected[3]	7.68	53.8	81.7	93.5	27.3	23	0.2440
Trial 2	226	1994, AI	75	surface	16.31	16.8	42.0	58.4	94.2	71	0.0342
				cross-section	9.46	16.3	44.3	68.1	76.9	68	0.2159
Trial 3	75	1994, AI	37	surface	8.11	65.3	89.3	93.3	19.5	11	0.0532
				cross-section	9.96	49.3	90.7	98.7	32.3	12	0.0012

[1] Percent CV = coefficient of variation × 100; CV calculated following Chang (1982).

[2] $P<0.05$ from Bowker's test indicates asymmetry of discrepancies between readers (i.e., reader bias).

[3] Corrected cross-section statistics from trial 1 are the result of a *post hoc* adjustment of reader 2's ages (see text).

age estimate increased by 4.7 years for 226 fish with mean length of 75 cm. The oldest surface age estimate was 28 years and the oldest cross-section estimate was 36 years (Fig. 3A). Maximum ages of Greenland halibut reported in the literature rarely exceed 20 years (Alton et al., 1988). These older ages result in smaller size-at-age and have the effect of decreasing estimates of von Bertalanffy's L_∞ (Fig. 4).

The older cross-section age estimates for Greenland halibut are consistent with natural mortality estimated by the gonadosomatic index method (M=0.112; Cooper et al., in press). Our maximum cross-sectioned age of 36 years indicates M = 0.115, as opposed to an M = 0.149 as indicated by the maximum surface age of 28 years (Hoenig, 1983). Current natural mortality parameters used in management are 0.18 in the Bering Sea and

Aleutian Islands (Ianelli et al.[6]) and 0.20 in the North Atlantic (Darby et al.[7]). These values are more consistent with surface age estimates.

We feel that age estimates made from stained cross sections are an improvement over surface age estimates for Greenland halibut. However, validation of the age estimates produced by these methods is necessary. Given the large discrepancies that we encountered in some specimens (10 to 20 years) these ages can be roughly tested with tag-recovery or radiometric methods.

The methods used in the present study may have application in other hard-to-age species. They are a practical alternative to serial thin sections because the preparation time is shorter and allows the method to be adapted for production aging. The embedding process also preserves the structure of fragile otoliths which can be damaged during the cutting and break-and-burn processes.

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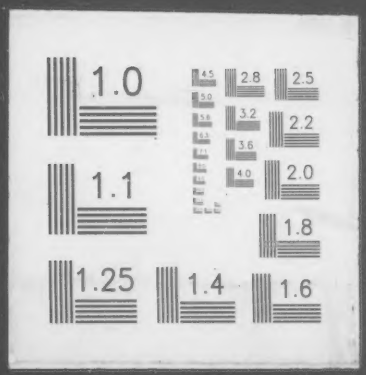
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